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OF LONDON.

1927, pp. 491-1009,

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THIS Society was founded in 1826 by Sir STAMFORD RAFFLES, Mr. J. SABINE, Mr. N. A. VIGORS, and other eminent Naturalists, for the advancement of Zoology and Animal Physiology, and for the introduction of new and curious subjects of the Animal Kingdom, and was incorporated by Royal Charter in 1829.

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The Meetings for Scientific Business are held in the Meeting Room at the Society's Office fortnightly on Tuesdays, except in July, August, September, and December and January, at half-past Five o'clock P.M.

The Anniversary Meeting is held on the 29th of April, or the nearest convenient day, at Four P.M.

The Society's Gardens are open daily from Nine o'clock until Sunset, or 8 P.M. when sunset is later. Dr. G. M. Vevers is the Superintendent, Mr. D. Seth-Smith, Curator of Mammals and Birds; Mr. Edward G. Boulenger is Director of the Aquarium; Miss Joan B. Procter, F.L.S., is Curator of Reptiles; Mr. L. C. Bushby, F.E.S., is Curator of Insects; Dr. John Beattie, M.B., Ch.B., M.Sc., is Anatomist; Dr. H. H. Scott, M.D., F.R.C.P., D.P.H., Pathologist; Prof. R. T. Leiper, F.R.S., with the assistance of a panel of experts, examines and reports on the Parasites; Prof. G. H. Wooldridge, F.R.C.V.S., is Honorary Consulting Veterinary Surgeon; and Dr. R. W. A. Salmond, O.B.E., Honorary Radiologist to the Society. Applications for anatomical or pathological material, or for facilities for work in the Prosectorium should be addressed to the Secretary.

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P. CHALMERS MITCHELL,

Secretary.

Regent's Park, London, N.W. 8.
January, 1928.

M E E T I N G S
OF THE
ZOOLOGICAL SOCIETY OF LONDON
FOR
SCIENTIFIC BUSINESS.

1928.

TUESDAY, FEBRUARY	7 and 21.
—— MARCH	6 „ 20.
—— APRIL.....	3 „ 17.
—— MAY	1 „ 15.
—— JUNE	5 —

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THE scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are issued in the volumes of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described therein. Amongst such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

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P. CHALMERS MITCHELL,

Secretary.

Regent's Park, London, N.W. 8.
January 1928.

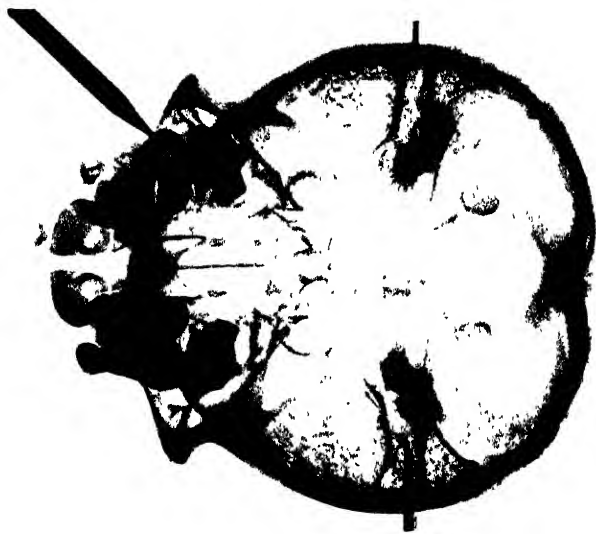
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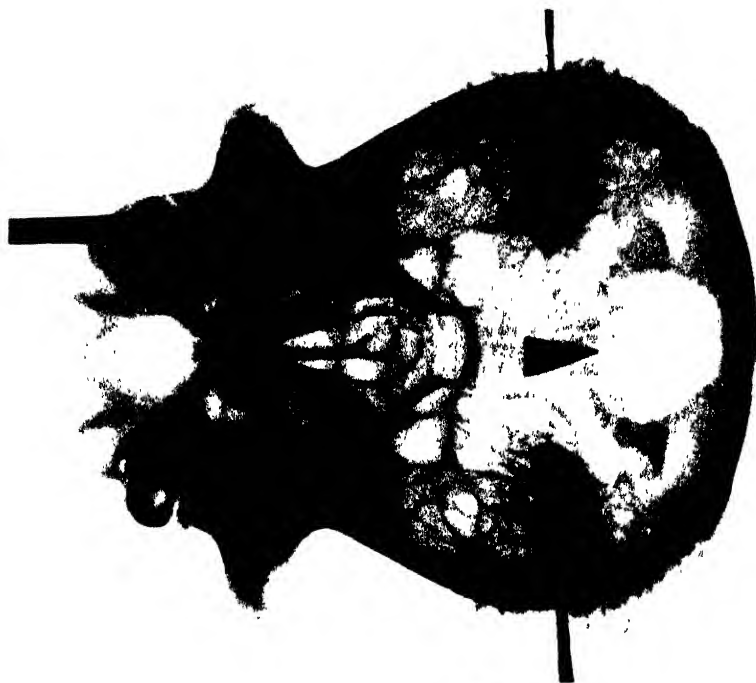
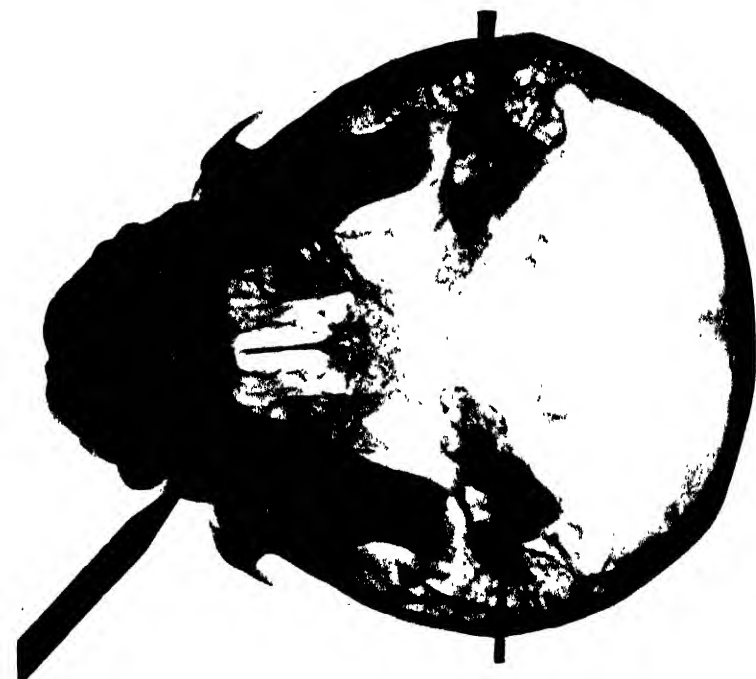


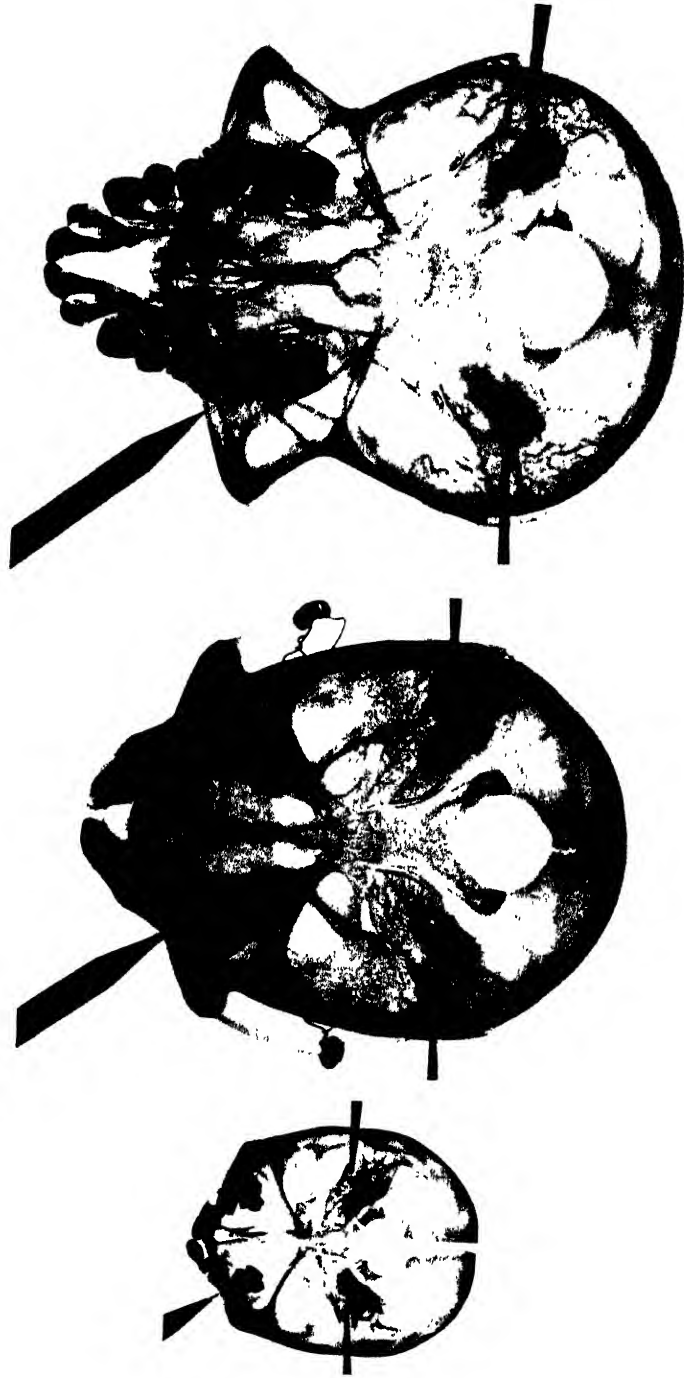
RADIOGRAPHIC NORMA BASALIS OF SEVEN GORILLA SKULLS



RADIOGRAPHIC NORMA BASALIS OF TWO CHIMPANZEE SKULLS

RADIOGRAPHIC NORMA BASALIS OF TWO ORANG SKULLS





RADIOGRAPHIC NORMA BASALIS OF THREE OLD WORLD MONKEYS

(1)



(2)



(3)



(4)



RADIOGRAMS OF MANDIBLES

PROCEEDINGS
OF THE
GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

ZOOLOGICAL SOCIETY OF LONDON

PAPERS.

31. The Skull, the Face, and the Teeth of Primates, with special reference to Dolichocephaly and the Centres of Growth in the Face.—Part I. By H. A. HARRIS, F.Z.S., Institute of Anatomy, University College, London.

[Received May 20, 1927: Read May 24, 1927.]

(Plates I.—VI.*)

A rapid method of obtaining the breadth-length ratio for the endocranial cavity of the dried skull was described recently by the author (1). This method, based on the radiography of the skull mounted in the Frankfurt plane, yields a *norma lateralis* and a *norma basalis* of known magnification. This method has the advantage of speed, simplicity and precision, and eliminates those errors which characterize actual measurements of the outside of the skull. The true endocranial dimensions are obtained irrespective of the varying degree of development of the air sinuses of the sagittal and occipital crests, and of the supraorbital crests.

The material included in this preliminary survey consists of 50 gorillas, 13 chimpanzees, 18 oranges, 5 gibbons, 26 Old World monkeys, 3 New World monkeys, and 2 lemurs. I am particularly indebted to Lord Rothschild (2) for the loan of the magnificent collection of gorilla skulls; to Professor Shellshear, of Hong Kong, and to Professor Le Gros Clark for orang skulls; and to Dr. Beattie, Anatomist to the Zoological Society, for most of the monkey skulls. My thanks are due to Mr. Melville, the departmental radiographer, for valuable help and assistance.

* For explanation of the Plates see p. 502.

The methods employed consist of the determination of :—

- A. The *Cranial Capacity*, by Flower's method of filling the skull with mustard seed and emptying the seed into a graduated cylinder by means of a large funnel, the stem of which was cut short, the bore at the exit being 2 cms.
- B. The *Facial Index* of Bolk (3). The greatest breadth is measured between the right and left points at which the zygomatic arch bends itself round into the orbital margin. The greatest length is measured in profile from the highest point in the mid-line of the crista supra-orbitalis to the anterior margin of the premaxilla between the central incisors.
- C. The *Endocranial Ratios* for length, breadth, and height. The maximum length of the skull is measured from the Fronton to the Occipiton of Bolk (3) on the radiogram of the norma lateralis (Pl. I.). The maximum height is measured from the Frankfurt plane to the highest point of the vertex on the radiogram of the norma lateralis. The maximum breadth is measured on the norma basalis. These three dimensions are reduced to the absolute by dividing by the factor of magnification of the radiogram. This method is checked by actual measurements on those skulls which happen to be sectioned in halves.
- D. The *Central Canal of the Chin*, the *Mental Foramina* and the *Infraorbital Foramina* have been surveyed.

Wherever a particular observation could not be made owing to the incomplete character of the skull, a blank space is left in the tabulated summary. A cipher, on the other hand, indicates absence in a complete specimen. In the case of multiple foramina, the number is indicated. In the case of the central canal of the chin, presence is indicated by the positive sign (+), and absence is indicated by a blank. The accompanying summaries (Tables I.-VI.) indicate the actual observations, with a statement of the average, maximum and minimum, for each group.

A.—CRANIAL CAPACITY.

The figures given for cranial capacity are, as Todd and Kuenzel (4) have pointed out, open to serious objection, for no method has an error of less than 3 per cent. A comparison of the cranial capacity recorded by other observers with the results here tabulated indicates that the range of variation is a very wide one, and that as the number of skulls examined increases, so the range of cranial capacity will extend. For example, Oppenheim (5) gives the range of cranial capacity in the gorilla as 370-585 c.cs. The Rothschild series extends from 366-625 c.cs., and Bolk records a capacity of 655 c.cs.

Table I.—GORILLAS (50).

No.	Cranial Capacity in c. cs.	Facial Index of Bolk.	Radiographic Endocranial Ratios.			Central Mental Canal.	Mental Foramen.		Infra-orbital Foramen.		
			B: L.	H: L.	H: B.		R.	L.	R.	L.	
Z.	35	366	116.6	81.5	67.2	82.8	+	1	1	2	1
A.D.	3	415	110.6	80.0	64.4	80.5		1	1	2	1
	8	420	102.4	86.8	63.1	72.7		1	1	2	2
	5	425	110.4	79.1	61.5	77.7		3	1	1	1
	6	430	110.9	84.2	62.5	74.2		1	1	2	2
	13	440	105.8	80.7	70.0	86.7		1	1	1	1
	34	140	111.1	76.6	65.9	86.0		3	1	2	2
	10	442	98.5	84.9	66.4	78.2	+	1	1	1	2
	4	450	114.6	78.3	61.9	79.0		1	1	2	2
	9	450	106.0	82.8	60.0	72.5		1	1	1	1
	41	455	105.0	82.5	61.2	74.2	+	1	1	1	1
	11	457	110.9	82.8	64.1	77.4		1	2	1	1
	17	460	111.3	80.3	63.1	78.6	+	1	1	2	3
	20	460	112.5	76.8	63.8	83.1		1	1	1	2
	1	460	96.2	85.2	64.3	75.5		1	1	2	2
	35	465	108.1	74.7	62.8	84.6		1	2	1	1
	21	470	109.1	77.2	59.8	77.5		1	1	2	1
C.A.	5	475	108.7	82.6	64.0	77.5		1	1	2	2
A.D.	36	480	104.1	79.5	65.1	81.9		1	1	1	2
	41	480	110.5	74.2	61.5	82.9		1	1		1
C.A.	2	490	129.2	80.5	61.8	80.5		1	1	2	2
A.D.	23	490	113.5	73.2	65.4	89.3	+	1	1	2	2
	19	495	111.8	80.8	59.4	73.5		1	1	2	3
	18	500	100.0	80.3	63.0	78.5		1	1	1	1
C.A.	4	510	111.0	84.7	67.2	79.3		1	1	1	1
A.D.	25	510	108.9	72.1	61.4	85.2		1	1	1	2
	38	520	97.9	76.0	62.0	81.6				1	1
	16	517	111.6	76.9	62.2	80.9	+	1	1	2	2
	14	550	113.7	74.4	56.6	76.1	+	1	1	2	2
	31	550	96.3	78.7	59.1	75.5		1	1	1	1
C.A.	1	560	110.9	84.7	64.0	75.6		1	1	1	1
A.D.	15	560	97.5	78.2	62.0	79.3		1	1	1	1
	40	560	125.3	72.7	56.2	77.3				2	1
	33	580	113.6	74.4	59.2	79.6		1	1	2	2
C.A.	2	652	129.2	80.5	64.8	80.5		1	1	2	2
A.D.	22		113.6	75.2	62.4	83.0	+	1	1	2	3
	24		120.8	76.6	67.1	87.6	+	1	1	1	2
	26		110.3	77.2	62.8	81.3		1	1	2	2
	27		113.6	81.1	62.4	76.9		2	1	1	2
	28		101.4	77.2	63.0	81.6	+	1	1	1	1
	29		110.4	79.7	65.7	82.4		1	1	2	1
	30		97.7	79.2	61.8	78.0		1	1	1	1
	32		111.4	74.0	57.4	77.6		1	1	2	2
	37		106.1	80.1	55.5	69.3				2	2
	39		92.9	76.0	58.7	77.2				2	
	42		97.5	81.4	64.1	78.7		1	1	2	2
	43		96.8	77.2	62.6	81.8				2	2
	45			75.0	60.3	80.4		1	1		2
	7		106.5	84.8	67.5	79.6		1	1	1	1
	12		107.5	79.7	58.9	73.7		1	1	2	2
No. of } Skulls. }	35	49	50	50	50			45	44	48	49
Aver.	486	180.1	79.3	62.7	79.4			1.11	1.04	1.56	1.6
Max.	652	129.2	86.8	71.4	87.6			3	2	2	3
Min.	366	92.9	72.1	55.5	69.3			1	1	1	1

Whereas most of the gorillas examined are adult, the chimpanzees, orangs, and monkeys in this series contain a large proportion of juvenile skulls, and the minimum capacity for the orang and gibbon falls short of the minimum given by Oppenheim.

Table II.—CHIMPANZEES (13).

No.	Cranial Capacity in c. cs.	Facial Index of Bolk.	Radiographic Endocranial Ratios.			Central Mental Canal.	Mental Foramen.		Infra-orbital Foramen.	
			B : L.	H : L.	H : B.		R.	L.	R.	L.
Z. 30	263	108.0	80.8	61.6	79.7		1	1	1	1
C.A. 14 d	279	104.9	80.4	71.8	83.1	+	1	1	1	1
13	283	112.9	83.0	65.1	78.4	+	1	1	1	1
B. 1	297	111.3	88.8	65.4	73.6	+	1	1	2	2
Z. 36	303	114.5	86.4	66.4	76.9				2	2
31	320	104.4	85.0	63.7	74.9		1	1	1	2
C.A. 14	340	117.6	91.7	69.4	75.7	+	1	1	2	2
14 c	341		83.3	59.7	68.1	+	1	1	3	3
14 a	347	115.1	82.8	60.7	73.3	+	1	1	2	3
14 b	357	105.1	79.7	59.3	74.4		1	1	1	2
Z. 39	357	110.6	85.3	68.1	79.8	+	1	1	1	3
C.A. 11	367	100.0	85.5	62.4	73.0		1	1	3	1
12	370	106.7	86.1	66.1	76.8	+	1	1	3	4
No. of } Skulls. }	13	12	13	13	13		12	12	13	13
Aver. ...	325	109.3	85.0	64.6	76.0		1	1	1.77	2.04
Max. ...	370	117.6	91.7	71.8	83.1		1	1	3	4
Min. ...	263	100.0	79.7	56.7	68.1		1	1	1	1

Table III.—GIBBONS (5).

No.	Cranial Capacity in c. cs.	Facial Index of Bolk.	Radiographic Endocranial Ratios.			Central Mental Canal.	Mental Foramen.		Infra-orbital Foramen.	
			B : L.	H : L.	H : B.		R.	L.	R.	L.
Z. 3	65	147.5	87.3	63.4	72.6		1	1	1	1
C.A. 43	66	166.7	75.7	56.8	75.0	+	1	1	1	1
42	71	159.4	82.9	62.9	75.9		1	1	1	1
31	90	166.7	86.5	58.1	67.2		1	1	2	1
Z. 33	96	134.1	84.6	64.1	75.8		1	1	1	1
No. of } Skulls. }	5	5	5	5	5		5	5	5	5
Aver. ...	78	151.9	83.4	61.1	73.3		1	1	1.2	1
Max. ...	96	166.7	87.3	64.1	75.9		1	1	2	1
Min. ...	65	134.1	75.7	56.8	67.2		1	1	1	1

B.—FACIAL INDEX OF BOLK.

Leptoprosopy, as distinct from chamæprosopy, occurs in nine gorillas, two orangs, and in one Old World monkey, which is *Papio hamadryas*. The gibbons are markedly broadfaced, and among the Old World monkeys this character reaches a

maximum in *Macacus fascicularis* and *Semnopithecus*. A comparison of the latter monkeys with the gibbon, the most primitive anthropoid ape, is much needed.

C.—RADIOGRAPHIC ENDOCRANIAL RATIOS.

The question of dolichocephaly in the Primates was revived by Dart's (6) interesting discovery of *Australopithecus africanus*. Dart, in describing this undoubted distinct genus of the ape family, says: "The whole cranium displays humanoid rather than anthropoid lineaments. It is markedly dolichocephalic and leptoprosopic." Keith (7) lays great stress on this character, and adds: "Even if it be admitted that the *Australopithecus*

Table IV.—ORANGS (19).

No.	Cranial Capacity in c. cs.	Facial Index of Bolk.	Radiographic Endocranial Ratios.			Central Mental Canal.	Mental Foramen		Infra-orbital Foramen.	
			B. L.	H. L.	H. B.		R.	L.	R.	L.
J.S. 8	259	120.0	91.7				2	1	2	2
7	270	120.0	90.6	72.9	80.4		1	1	2	2
L.G.C. 3	272	105.7	100.0	68.0	68.0		1	1	2	3
J.S. 6	281	130.4	92.1	73.0	79.3		2	2	2	3
L.G.C. 4	311	114.1	86.2	67.2	78.0		1	1	3	3
J.S. 3	320	118.0	89.6	69.6	78.9		1	1	2	2
4	330	109.2	81.3	67.6	80.2		1	1	1	1
C.A. 22	339	123.3	86.1	60.0	60.7		1	1	2	2
21	339	96.4	88.8	64.8	73.0		1	1	3	2
23	350	114.6	88.7	70.4	79.3	+	1	1	2	2
R. 2	351	100.0	90.1	77.5	86.0		1	1	3	3
C.A. 25	355	104.1	80.2	63.8	79.6		1	2	3	2
J.S. 5	363	103.5	90.8	73.1	80.5		2	2	2	3
Z. 32	400	103.4	86.4	66.9	77.1		1	1	5	4
29	402	112.4	81.5	70.6	86.6		2	4	3	2
R. 3	409	91.2	80.5	61.0	75.8	+	3	3	3	3
J.S. 2	420	105.3	89.0	67.0	75.3		2	2	2	2
1	425		86.9	67.2	77.3		1	1	1	2
No. of } Skulls. }	18	17	18	17	17		18	18	18	18
Aver.	345	110.1	87.9	68.3	77.4		1.39	1.5	2.39	2.39
Max.	425	130.4	100.0	77.5	86.6		3	4	5	4
Min.	259	91.2	80.2	60.0	68.0		1	1	1	1

is an anthropoid ape, it is a very remarkable one. It is a true long-headed or dolichocephalic anthropoid—the first so far known." Bolk (3) has published a description of the sole dolichocephalic gorilla in the Amsterdam collection of fifty skulls. Oppenheim had previously recorded two cases of dolichocephaly in the gorilla. In the Rothschild series of gorilla skulls here examined, dolichocephaly is seen in eight skulls out of fifty. The eight dolichocephalic skulls are distinct from the nine leptoprosopic skulls, so that there is no close correlation between these two characters of head-length and face-length. However, Bolk's dolichocephalic gorilla was also

Table V.—OLD WORLD MONKEYS (26).

No.	Cranial Capacity in c. cs.	Facial Index of Bolk.	Radiographic Endocranial Ratios.			Central Mental Canal.	Mental Foramen.		Infra-orbital Foramen.	
			B : L.	H : L.	H : B.		R.	L.	R.	L.
Z. 22	49	104.2	79.7	57.4	68.6	+	2	2	4	4
17	55	128.6	74.6	59.7	80.0		1	1	3	3
14	62	127.8	75.3	54.8	72.8	+	1	1	2	3
12	63	123.7	76.1	56.3	74.0	+	1	1	4	3
9	64	124.4	81.4	57.1	70.1	+	1	1	2	2
10	65	119.5	77.0	56.8	73.8	+	2	1	2	4
4	68	125.0	76.3	52.6	68.9		1	1	3	2
8	68	119.5	80.0	60.0	75.0	+	1	1	3	3
C.A. 46	68	153.5	83.8	61.8	73.7		1	2	3	3
Z. 28	69	118.0	75.7	55.5	73.7	+	1	2	2	3
6	71	129.3	80.3	60.6	75.5	+	1	2	3	2
16	72	111.1	79.5	54.8	68.9		1	1	3	3
5	73	120.9	75.7	58.1	76.1	+	1	1	3	4
C.A. 45	75	121.7	80.6	62.5	77.5	+	2	2	3	3
Z. 21	75	114.0	85.9	62.0	72.2				3	4
13	77	120.0	77.3	53.3	69.0	+	1	1	3	3
2	78	110.0	75.6	52.6	69.6	+	2	2	4	2
11	78	119.0	76.0	56.0	73.7	+	2	1	2	2
1	80	109.8	79.7	59.6	74.8		2	2	3	2
15	80	120.7	81.1	56.8	70.0	+	1	1	3	3
3	84	122.9	76.3	55.0	72.1	+	1	1	3	3
7	85	140.0	74.6	56.4	75.6	+	2	2	2	3
19	90	123.3	77.2	57.0	73.8	+	1	1	3	2
C.A. 44	97	150.0	96.3	57.5	69.7	+	1	1	3	2
Z. 20	98	125.0	79.7	59.5	74.7		1	3	5	4
18	160	76.5	83.5	58.2	69.7		3	3	4	4
No. of } Skulls. }	26	26	26	26	26		25	25	26	26
Aver. ...	77.1	121.5	79.2	57.3	72.5		1.36	1.48	3.0	2.92
Max. ...	160	153.5	96.3	62.5	80.0		3	3	5	4
Min. ...	49	76.5	74.6	52.6	59.7		1	1	1	1

Table VI.—NEW WORLD MONKEYS (3) and LEMURS (2).

No.	Cranial Capacity in c. cs.	Facial Index of Bolk.	Radiographic Endocranial Ratios.			Central Mental Canal.	Mental Foramen.		Infra-orbital Foramen.	
			B : L.	H : L.	H : B.		R.	L.	R.	L.
Z 23...	12	130	75.0	52.3	69.7				1	2
24...	26	103.1	80.4	58.8	73.1		1	1	2	2
26...	59	134.3	75.0	61.8	62.4		1	1	2	2
Z 25 ..	18	117.5	77.6	55.1	71.0		1	2	1	1
Z 27 ..	23	114.6	80.0	56.0	70.0		3	2	1	1

leptoprosopic. The endocranial breadth-length ratio in the Rothschild series of gorillas ranges from 72.1 to 86.8 (Pl. II.). This range is of the same order as that which occurs in Man. Oppenheim's series of gorillas ranges from 70.4 to 94.2, but

these indices are not based on sound endocranial measurements. Keith (7) has estimated the breadth-length ratio in *Australopithecus* as 71 and Hrdlicka (8) as 74. Reference to Tables II. and IV. show that the young orangs are markedly brachycephalic, and the young chimpanzees are moderately so. There is no case of dolichocephaly in the chimpanzees or orangs, but one of the gibbons has a ratio as low as 75.7, which suggests that a larger number of gibbons would yield several cases of dolichocephaly. Two of the Old World monkeys (*Macacus rhesus*) are clearly dolichocephalic, and the condition will be met with in any extensive series of New World monkeys and lemurs. The norma basalis of several specimens is shown in Pls. III.-IV. It is clear that dolichocephaly, *per se*, cannot be applied with any degree of certainty to the problems of classification.

The auricular height-length ratios, as determined by the radiographic method, show that the gorilla is orthocephalic, and is intermediate in position between the relatively hypsicephalic orang and chimpanzee on the one hand, and the chamacephalic monkeys on the other hand. There is no well-marked change in the height-length ratio with age in the series of orangs and chimpanzees. The orang, with a brachycephalic and hypsicephalic skull, shows the nearest approach to the "turmschadel" which is occasionally seen in the human, or commonly in the Armenoid type. In Man the range of the auricular height-length ratio is given by Martin (9) as 60.3 to 77.5.

The average values of the ratios are tabulated as follows:—

	B. L.	H : L.	H : B.
Man	77.8	68.9	88.5
50 Gorillas ...	79.3	62.7	79.4
13 Chimpanzees	85.0	64.6	76.0
18 Orangs	87.9	68.3	77.4
5 Gibbons	83.4	61.1	73.3
26 Old World Monkeys ...	79.2	57.3	72.5

D (1).—THE CENTRAL CANAL OF THE CHIN.

The central canal of the chin in Man has attracted but little attention since the first description thereof in 1900 by Bertelli (10). Sir George Thane (11), in 1899, said in reference to the genial tubercles on the deep surface of the human symphysis menti, "above the upper spines a small median foramen penetrates the bone." Bertelli first showed that this foramen leads into a central canal of the chin, which sometimes opens on the outer surface of the chin in the mid-line. He described this canal as completely traversing the symphysis in 3 out of 380 Italian mandibles. Le Double (12) described 2 cases in 300 mandibles, and Dubreuil-Chambardel (13) one case in 75 mandibles. Thiele (14) and Rojecki (15) found that in monkeys this median canal is traversed by a branch of

the lingual artery *via* the sublingual branch. This artery supplies the bone in the neighbourhood of the symphysis and anastomoses with the twigs of the submental branch of the external maxillary (facial) artery. Mr. Wilfred Trotter (16), in a personal communication, states that a small lymphatic gland is occasionally seen in Man near the foramen on the deep surface of the mandible, so that it appears that the canal serves as a communication between the vascular and lymphatic territories of the sublingual and facial arteries. This may be a matter of some import in the spread of carcinoma of the tongue. According to Le Double this canal occurs in lower monkeys and Rodents, and several vestigial foramina with incomplete canalization of the mandible occur in the Carnivora. On the other hand, Le Double states that an examination of 22 chimpanzees, 17 oranges, 16 gorillas, and 7 gibbons showed nothing but vestiges of the central canal.

In the series of Primates here examined, a completely pervious central canal of the chin, traversing the whole thickness of the mandible, occurs in 10 gorillas, 8 chimpanzees, 2 oranges, one gibbon, and in 16 Old World monkeys (Pl. VI.). The canal is absent in the Old World monkeys and lemurs. In some cases the canal is Y-shaped, with one opening on the superficial aspect and two openings in the deep aspect of the mandible. Dr. Beattie (17) has confirmed the existence of a blood-vessel in one chimpanzee by injection of the lingual artery, and he finds that the vessel is an anastomotic branch between the sublingual and external maxillary. The development of this central canal and its contained vessels may throw some light on the problem of the degree of fusion of the anterior ends of the Meckelian cartilages, on the fusion of the ossa dentalia, and on the development of the mental ossicles. The peculiar configuration of the upturned anterior extremities of the Meckelian cartilages in the human embryo have recently been described by Bolk (18), and it would appear that the canal is formed between the fused Meckelian cartilages above and the right and left ossa dentalia below.

D (2).—THE MENTAL FORAMINA.

The first description of multiple mental foramina in Primates was that of Patruban (19), who described a human mandible presenting two foramina on each side. Later, Gruber and Bertelli described human mandibles with three foramina on each side. Serres, Cruveilhier, and Rambaud and Renault had depicted mandibles with accessory foramina many years before, and, in their famous atlas, Rambaud and Renault figure the condition in a human foetus. Le Double (20), in his summary of the comparative anatomy of multiple mental foramina, said that the condition is normal in the whale, dolphin, pig, camel, dog, cat, bat, and in many monkeys; the higher

monkeys and apes tend to show a reduction to a single foramen.

Simonton (21), in a recent survey of the mental foramina in Man and anthropoids, gives the distribution of mental foramina as follows:—

20 Gorillas,	2 or 3 foramina in	27 per cent.
14 Chimpanzees,	„ „	15 „
61 Orangs,	„ „	39 „

In our series the distribution of multiple foramina is much less frequent than in Simonton's material at the Smithsonian Institute. Reference to Tables I.-VI. shows that multiple foramina are seen in but five gorillas, and that on one side only. The chimpanzees are constant in the possession of but a single foramen, and the orangs alone show a close resemblance to Simonton's data. One half of the Old World monkeys have bilateral single foramina. The wide discrepancy shown by the two series illustrates very clearly the need for a number of observations on a much larger number of specimens.

The Primates may be arranged in a series in order of approximation to the single mental foramen as follows:—chimpanzee, gibbon, gorilla, Old World monkey, orang, lemur. In the fossil Adapidae there are usually three mental foramina, and Gregory (22) has shown that in the fossil *Notharctinae* there is usually a fourth mental foramen. If, as Gregory states, *Notharctus* is a little-changed survivor of the primitive lemuroid stock which gave rise to all the higher primates, it would appear that the reduction in number of the foramina has progressed to almost the same degree in the chimpanzee as in Man, for Le Double gives the frequency of the condition in the latter as over 3 per cent.

D (3).—THE INFRAORBITAL FORAMINA.

Winslow (23), in his classical text book, described duplication of the infraorbital foramen in Man as early as 1732. Gruber (24) and Le Double (25) have studied the wide variation in the number of foramina associated with the infraorbital branch of the maxillary division of the fifth cranial nerve. Le Double describes a range from eight in the whale, five in the baboon, to four in the apes. In the latter, he adds, it is not rare to find a single foramen. Inspection of Tables I.-VI. show that single foramina occur bilaterally in 16 gorillas, 3 chimpanzees, 1 orang, 4 gibbons. In the Old World monkeys the foramina are multiple in all cases. Keith (26) states that the partition between two foramina on the one side is vertical in the gorilla and horizontal in the chimpanzee. Sonntag (27) says that the very first chimpanzee examined by him had a vertical septum. Similarly, the first gorilla in our series had a horizontal septum. Careful examination of the whole series shows that

the inclination of the septum between the two foramina, and its width, is very variable. The relative positions of the multiple foramina may be determined by several factors, of which but one can be definitely postulated. In infancy the foramina tend to be arranged horizontally below the infraorbital margin. As age advances, the foramina tend to be carried into relative positions which alter *puri passu* with the growth of the upper jaw. This process is still more accentuated with the eruption of the permanent dentition. In the extreme leptoprosopic gorillas the two foramina are arranged almost one above the other. In the chamæprosopic gorillas they are arranged almost side by side. In the intermediate forms the lateral foramen is also inferior to the median foramen, and all degrees of obliquity can be seen in the series of 50. The same applies to the multiple foramina in the chimpanzees and gorillas. The relative position of the foramina varies with the degree to which the upper jaw becomes precerebral, as distinct from its embryonic subcerebral position. An extreme example is afforded by *Papio*, in which there are five or six foramina arranged from behind forwards on the large upper jaw. The gibbon, on the other hand, tends to have a single foramen, and the Old World monkeys tend to have 3 or 4 foramina arranged side by side. In Man the foramen is single in more than 99 per cent. of the cases.

The infraorbital canal in the gorilla is shallow, and is not extensively arched over with bone except in its anterior third. In the chimpanzee and orang the canal is deep, with overhanging margins, and is arched over with bone in its anterior third, in its posterior third, and sometimes in its entirety, thus approximating to the position found in Man. On the other hand, the gibbon, with its single infraorbital foramen, has but a short bony canal near the margin of the orbit, and no trace of a canal in the posterior portion of the floor of the orbit. It is proposed to give a survey of the other foramina of the face in a further communication, with a view to checking the Retardation-hypothesis of Anthropogenesis of Bolk (28) and the theory of the Persistence of Primitive Simplicity, as enunciated by Elliot-Smith (29).

SUMMARY.

(1) The author's radiographic method of determining the form of the endocranial cavity of the skull has been applied to a large series of Primate skulls. Leptoprosopy and dolichocephaly are shown to be normal features of certain Primates. The degree of dolichocephaly in the Gorilla is as great as that in Man, so that dolichocephaly, *per se*, cannot be regarded as a humanoid feature.

(2) The central canal of the chin is shown for the first time to be a normal but inconstant feature of the mandible of Primates.

(3) Mental and infraorbital foramina are analysed with special reference to their multiplicity, their relative position, and the associated direction of growth in the upper jaw and mandible.

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EXPLANATION OF THE PLATES.

PLATE I.

The radiographic norma lateralis of the Orang, J.S. 2, showing the clearness with which the Fronton and Occipiton of Bolk are displayed.

PLATE II.

The radiographic norma basalis of seven Gorilla skulls, showing the variation in skull-form.

The endocranial breadth : length ratios are:—

Top Row—A.D. 40=72·7. A.D. 14=74·4. A.D. 25=72·1.

Bottom Row—C.A. 2=80·5. A.D. 1=85·2. A.D. 8=86·8. A.D. 23=76·6.

PLATE III.

The radiographic norma basalis of two Chimpanzee skulls.

Endocranial breadth : length ratios:—

C.A. 14=79·7. C.A. 14=91·7.

PLATE IV.

The radiographic norma basalis of two Orang skulls.

Endocranial breadth : length ratios:—

J.S. 5=90·8. J.S. 8=91·7.

PLATE V.

The radiographic norma basalis of three Old World Monkeys.

Endocranial breadth : length ratios:—

Z. 17=71·6. Z. 7=74·6. C.A. 14=96·3.

PLATE VI.

A series of radiograms with a fine brass wire passing through the central mental canal of the mandible.

A.D. 23, Gorilla; Z. 18, *Papio hamadryas*; Z. 5, *Macacus rhesus*;

Z. 20, *Macacus nemestrinus*.



FIG 1

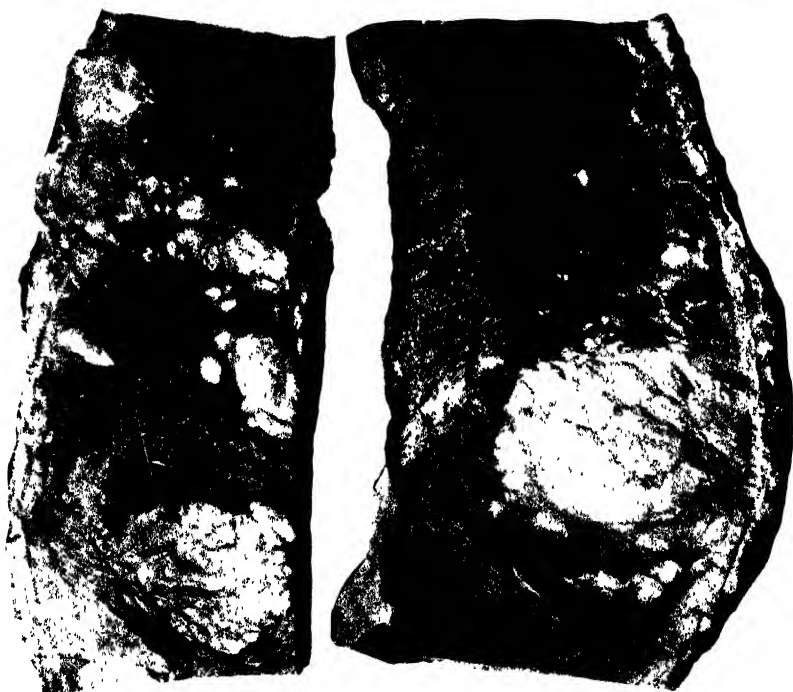


FIG. 2

NEOPLASM IN AN INDIAN RHINOCEROS.



FIG. 3

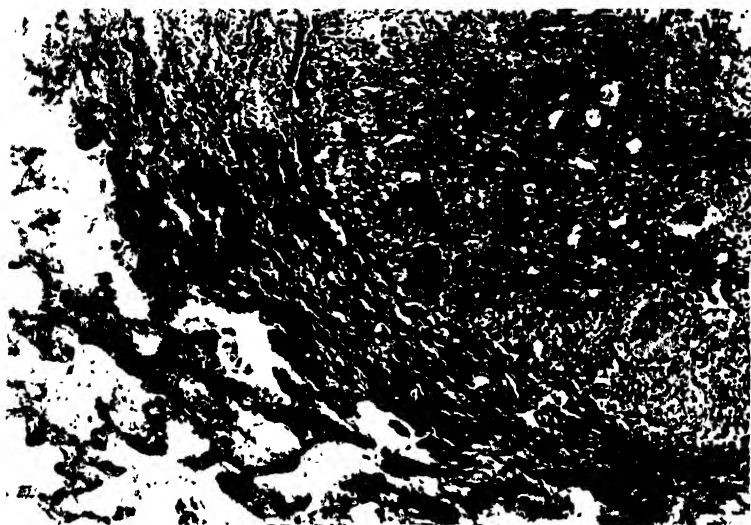


FIG. 4

NEOPLASM IN AN INDIAN RHINOCEROS.

32. Neoplasm in an Indian Rhinoceros (Sarcoma of Heart and Lungs). By H. HAROLD SCOTT, M.D., F.R.C.P. London, F.Z.S., Milner Research Fellow in Comparative Pathology, London School of Hygiene and Tropical Medicine; Pathologist to the Society.

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(Plates I., II.*)

The case here recorded is that of an Indian Rhinoceros (*Rhinoceros unicornis*) from Nepal. It was brought to the Gardens as quite a young animal on April 7th, 1922, and had always been in excellent health until the beginning of April 1926, when it was noticed to be losing its appetite. There were no other symptoms, and when seen on the evening of April 27th, though it refused food, it was not considered to be any worse than during the preceding days. The following morning, however, at 6 A.M., it was observed to be in much distress and died quite suddenly a few minutes later.

The post-mortem examination was started about three hours afterwards, and the findings were as follows:—

There was bleeding at the nose, thought to be due to injury sustained in falling at the moment of death: a slight anal prolapse was present, but no other external signs worthy of note.

On opening the body, the striking feature was the size and the general appearance of the heart. The pericardial cavity contained about 3 litres of slightly blood-tinged yellowish fluid; the membrane was not inflamed, nor thickened as a whole, but on its visceral surface were several nodules of new growth, more closely aggregated towards the base of the heart.

The anterior surface of the heart itself presented an enormous number of small nodular deposits, covering practically the entire surface (Pl. I.); some of them showed small hæmorrhages. They appeared to be most thickly aggregated over the right auricle, but were very numerous all over. The posterior surface of the heart also showed many deposits, but considerably less than were visible on the anterior aspect, covering in all about one-third of the surface and aggregated more towards the upper part, the base, of the heart.

On cutting open the heart, it was seen that the growths were not merely superficial. The wall of the right auricle was crowded with tumour-masses, and infiltration had extended

* For explanation of the Plates, see p. 510.

through to the surface. All the chambers showed that the thickness of the myocardium had been involved. Some of the masses in the left ventricular wall were as large as a golf-ball, and one even larger (Pl. II.). They give the impression from their position and relations of having arisen from without and extended inwards, rather than by embolism from within. Possibly, from the greater aggregation in the right auricle, this had been the first part of the heart to be attacked, and thence the growth had spread to involve the pericardium with resultant rapid, local or contiguous extension.

Some of the deposits in the wall of the right ventricle were more distinct on the internal surface and did not reach through to the outer. It is possible, perhaps probable, that these had arisen from fragments being carried from the right auricle to the ventricle and there developing.

The thymus was represented by remnants of tissue only, and the thyroid was normal.

The right lung contained a large deposit of growth near its root, the mass of the tumour being the size of a Tangerine orange. There were also several very minute, whitish deposits scattered irregularly through the lungs. The same remark applies to the left lung, while in the lower lobe, about the middle, there was a single mass as large as a cherry. The bronchial glands were not enlarged.

The minute deposits proved on microscopical examination to be each a small nodule of growth, as if there had been a number of emboli from the mass in the left auricle whipped off into the pulmonary circulation.

Thus would be accounted for the fact that embolic tumours were not found in any of the other viscera, liver, spleen, kidneys, etc.; in other words, the systemic circulation had not been invaded.

The only other condition of which mention should be made was that the intestine was somewhat acutely inflamed, the mucosa showed a few petechial hæmorrhages, while some areas were more uniformly red and blood-stained. In the peritoneum the fluid was in excess, though not measurable, and there were small masses of gelatinous coagula.

The liver was mottled and, on section, was seen to be "foamy," the tissue spongy and soft and the spleen, though not enlarged, was also softer than normal and frothed a little on section. The mesenteric glands were swollen and congested. Welch's bacillus—*B. aerogenes capsulatus*—was grown by anaerobic culture from the liver, spleen, and heart-blood.

There was no swelling or softening of the bones noted at the autopsy, and subsequent maceration for the purpose of preparing a skeleton showed a splendid condition of all the bones, no abnormal localised swellings.

Histological examination.

Section of the *Heart* when viewed by a low power, such as a hand-lens, showed several small foci which appear as if separate and, in a way, encapsulated. Under higher magnification, however, it is seen that there is no true capsule, though the periphery is more fibrous than the interior and the surrounding tissue is compressed; at the same time this is fairly heavily invaded by small round cells. In more minute detail, the *stroma* varies in amount in different foci and in different parts of the same focus. In some situations there are many small round cells and little stroma, but over the greater part there is relatively abundant stroma, some of it of hyaline aspect, but made up of very fine fibrils, interspersed with elongated cells which have relatively large oval, or, more often, spindle-shaped nuclei.

The characters of the *cells* are those of a mixed large and small round-celled sarcoma, among which the latter greatly preponderate. A considerable number of the larger show mitotic figures.

In each of the foci of growth there are numerous *giant-cells*. Here and there may be seen one showing slight vacuolation, and others show a sort of tear or cleavage due probably to shrinkage in the preparation of the tissue. The giant-cells vary considerably in size, but in almost every case the edge is smooth and regular, nothing of the nature of the processes found in osteoclasts being seen. The nuclei are present in large numbers, some containing a hundred or more; they are situated centrally or dispersed through the cell, not peripherally, nor are they of a uniform size in a cell and several show mitotic figures.

Nowhere in any of the sections is there anything suggestive of bone-formation; within the tumour-nodules themselves no hæmorrhages have been seen, though extravasations are found at the periphery in certain parts.

Occasionally one can make out degenerated heart-muscle cells in the interior of the tumour nodules, especially at the periphery.

As regards the deposits in the *Lungs* the capsule-appearance is rather more marked and the fibrous stroma more prominent, especially at the periphery, where it is more dense, though infiltrated by round cells several of which show mitosis. The disposition of the stroma is very similar to that already described in the case of the tumours in the heart; that is, it exhibits considerable variation in amount, some areas showing very little and consisting almost entirely of small round cells with faint, fibrillar intercellular stroma, others with an alveolar arrangement, a little denser fibrous stroma arranged as a mesh, containing small round cells between which are the faintly-staining fibrils; giant-cells are numerous, rarely is any seen with vacuolation, the nuclei are many and resemble in all respects

those in the heart. At the periphery of the tumour-nodules the pulmonary tissue appears compressed and the alveolar walls thickened, and there is a fibrosis invaded by numerous small round cells. Here, as in the heart, no extravasations are seen within the deposits themselves, but in parts, particularly at the periphery of the nodules, the pulmonary tissue may show extensive foci of hæmorrhage, the alveoli being filled with corpuscles and shed cells; there is no broncho-pneumonia in the compressed parts of the lung.

Discussion.

The problem offered by this interesting case is the solving of the question as to the source of these tumours. There can be no doubt, from their enormous number in both heart and lungs, that in the case of each organ the deposits are secondary. The fact that extra-cardiac tumours were found only in the lungs is evidence that dissemination in the latter came by way of the pulmonary artery. This is borne out by the further fact that, though the tumours are widely distributed over the surface of the heart, the chamber most heavily involved is the right auricle which, as already stated, is crowded with growth and its wall infiltrated throughout. Fragments have, in all probability, been carried from the auricle to the ventricle and thence distributed as emboli throughout the lungs, which have become studded with minute sarcomatous deposits and others of greater size, as would result from repeated embolism.

Again, the wall of the auricle consisting as it does, of a mass of agglomerated deposits, has transmitted the cells to the overlying pericardium, and when once this was reached the spread would naturally be a rapid one by contiguity over the whole surface over the heart and its serous covering.

Primary malignant tumours of the heart, non-malignant also for that matter, are very rare, and in this instance may be excluded by their very number. If it be suggested that there was some primary growth in the heart which had extended to involve the pericardium and produce such generalized infection of the whole organ, we can only say that, if possible, such is highly improbable, because while all this local mischief was developing we should expect to find signs of embolic distribution of tumours in the parts supplied by the systemic circulation.

Regarding the condition of the heart, then, as secondary, we are confronted with the problem of the site of the primary growth. In most cases of cardiac neoplasm, when these are present in any number, the primary growth is probably the mediastinum, the pericardium becoming invaded, and the growth spreading thence to the myocardium. Sarcoma of the thymus may so extend. In the present case, however, there was no

growth seen in the mediastinum and the thymus was specially observed, as there was no knowledge of the age of the animal, except that it was believed to be a young one. The gland, however, had almost disappeared, being represented only by remnants of tissue.

Giant-cell sarcomata, as sources whence the heart becomes involved, have been reported in the mammary and thyroid glands (Hektoen and Riesmann), but these sites were examined and found free from disease.

We may, therefore, set aside any adjacent organ as the site of the primary growth.

The commonest source of origin of secondary tumours of the heart is unquestionably bone, and in the case of this Rhinoceros the histological picture with its preponderance of giant-cells in all the sections made tends to support this argument.

It is, of course, well known that too much importance in this respect must not be paid to the existence of giant-cells in a tumour. They are not uncommon in both spindle- and round-celled sarcomata, especially in the larger-celled examples. All the sections made from tissue taken from various parts of the heart and lungs in this case, however, show that, except for the numerous giant-cells, the majority of cells are of the small round type. Wherever these giant-cells are found in large numbers the question as to their significance is always a matter for debate. There are four possibilities to be considered, namely:—(1) Are they merely "foreign body" giant-cells? (2) Are we dealing with a myeloid sarcoma, secondary to or arising primarily from bone-reticulum? or (3) with a myeloma, arising from bone-marrow or, lastly, (4) with a "giant-cell sarcoma"?

The first can be disposed of in a few words; such cells are generally found in necrosing or degenerating areas, and are probably of endothelial or leucocytic origin. They do not attain the size of those present in sections of the tissues in this case, and in the great majority of them the nuclei are polar, or peripherally disposed. This was very exceptionally seen here; as mentioned already, the nuclei were either central or distributed generally throughout the cytoplasm.

A considerable degree of confusion exists as to the differences between myeloid sarcoma, myeloma, and giant-celled sarcoma of bone, which Professor Kettle has done much to elucidate. We need not go into the differences in detail here; suffice it to say that the first arise in the interior of bones (except epulis) and, in particular, certain parts of certain bones—adjacent ends of tibia and femur, upper end of humerus and lower end of radius. They expand and absorb bone rather than infiltrate it, are very vascular, and may pulsate, are often discoloured from hæmorrhage, and are, in a way, locally

malignant, but seldom if ever become disseminated. The giant-cells are of the osteoclastic type, having regular nuclei which do not show signs of abnormal activity. Such were not the characteristics, already given, of the giant-cells of the tumours in the Rhinoceros. Further, the giant-cells differ from those designated foreign-body giant-cells in that the nuclei are not arranged peripherally, there is no central degeneration; in fact, they are the analogues of the myeloplaxes normally found in bone-marrow. In such tumours there is a tendency to the formation of bone-spicules, and the cells generally are of the fibroblastic type, though often somewhat irregular in shape.

The second, myeloma, is by some authors regarded as synonymous with the last, and others who do not definitely state this as a fact are, judging from their descriptions, of the same opinion. According to Kettle, several of these tumours may develop simultaneously, or there may be a single growth at first, rapidly succeeded by others, but always in the bony skeleton, vertebræ, ribs, limb-bones, etc. The constituent cells are myeloblasts, or possibly plasma-cells, but the large cells of the osteoblast type, cells typical and characteristic of the myeloid sarcoma, do not occur.

Lastly, there remains the so-called Giant-cell Sarcoma. Some authorities dispute the existence of such a tumour as a distinct entity, regarding the giant-cells as either foreign-body cells or as modifications of the tumour-cells proper resulting from lack of cell-division and irregular mitosis, and common to neoplasms of various kinds, endothelioma, carcinoma, etc. Others, on the contrary, maintain that, though large multinucleated cell-masses occur at times in many sarcomata constituted by a mixture of cells, spindle- and round-celled, large or small, there is also a group in which these giant-cells are so constant and numerous as to form a characteristic feature and these are placed apart as Giant-cell Sarcomata. In the former, the mixed-cell sarcomata with giant-cells, the intercellular fibrillated stroma is usually scanty and any vessels present are of rudimentary form. It is true that such have been found in the majority of cases to arise primarily in connection with osseous tissue, and should, therefore, be classed with the osteosarcomata, but in others there is no apparent tendency to the formation of bone or cartilage. Among the latter there are met with sarcomata whose predominant constituent cells (apart from the giant-cells) are of the round-cell type, whose stroma is small in amount, finely fibrillated, but which may in some situations be disposed in definite fibrous trabeculæ enclosing the round cells, and, in fact, constituting a form of alveolar sarcoma or, yet again, showing in parts a more uniform, almost homogeneous material believed to be a secretion from the cells. Such tumours differ from the myeloid sarcomata, previously mentioned, in two important

particulars—namely, that the giant-cells vary considerably in the size of their nuclei and in their exhibiting abnormal mitoses, and that careful search will often reveal, as it were, transitional forms between the smaller cells of the tumour and these large multinucleated giant-cells.

To sum up the somewhat confused question of sarcomata of bone: It would appear that the majority of less malignant are of the spindle- or mixed-cell type containing giant-cells in varying number, some of the latter showing the general conformation of myeloplaxes. If arising from the periosteum tumour-formation in its strict sense is early in evidence; if from the interior—central sarcoma—they grow and slowly erode the framework of the bone, gradually replacing the bony tissue by the tumour-mass till spontaneous fracture results or attention is called to the bony swelling with pulsation and, perhaps, the characteristic “egg-shell” crackling.

Others contain a greater admixture of round-cells as the predominant cell of the groundwork, and so take on, as it were, a more truly sarcomatous character, namely that of small round-celled sarcomata which, whatever their situation, are generally regarded as the most malignant of these tumours. They probably give rise in their earliest stages to a certain degree of bone-erosion, but insufficient to cause any swelling recognizable externally; in fact, their malignancy is shown by early dissemination before there has been time for the local tumour to develop.

There is, it is true, a considerable degree of hypothesis in applying this reasoning to the case which forms the subject of this paper. Examination at autopsy revealed no primary tumour to which the secondary deposits in heart and lungs could be traced, and even after maceration for the setting up of the skeleton none of the bones showed the least deformity. Nevertheless, seeing that the commonest origin of secondary tumours of the heart is bone, that the neoplasm in this case contained numerous giant-cells, that the groundwork was of small round-cells, the most satisfactory, or perhaps we should say the least unsatisfactory, explanation would appear to be that there was some small round-celled endosteal sarcoma which became disseminated before any recognizable tumour had developed sufficiently to declare itself locally. This could only be proved by sections being made of all the bones of this animal, a matter now beyond our reach.

I wish to express my indebtedness to Mr. F. Martin Duncan and to Mr. F. W. Bond, the former for the photographs of the microscopic specimens, the latter for the macroscopic.

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. The anterior surface of the Heart showing vast numbers of nodules of growth.
- Fig. 2. Sections through the Left Ventricle of the heart showing one large and several smaller sarcomatous deposits.

PLATE II.

- Fig. 3. Section of small nodule of growth in the heart showing the giant-cells, both central and peripheral, with infiltration at the border by small round-cells also, where invasion is progressing.
- Fig. 4. Section of nodule in Lung. Note the large number of giant-cells in the main mass and the fibrosis at the periphery which gives the idea of encapsulation to the naked eye. This tissue is, however, fairly densely invaded by small round-cells and also by giant-cells. To the left are seen the pulmonary alveoli into the meshes of which round-cells are penetrating. There is no evidence of bronchopneumonia.

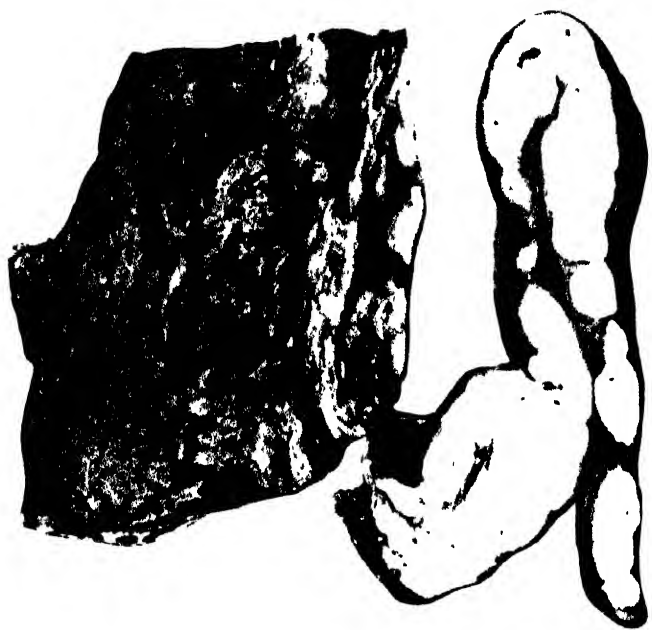


FIG 1



PERITONEAL NEOPLASM (ENDOTHELIOOMA)

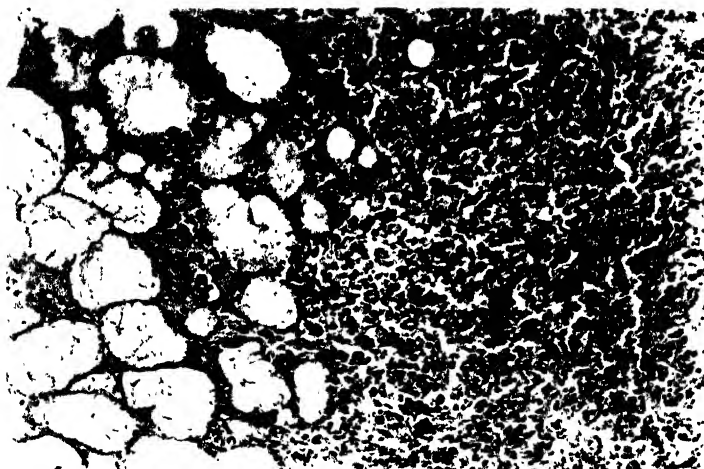


FIG 2



FIG 3

PERITONEAL NEOPLASM (ENDOTHELIOMA).

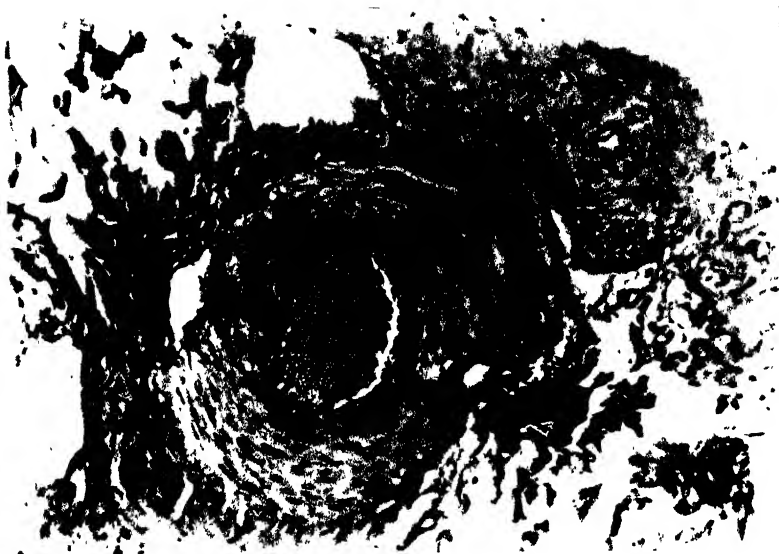


FIG 4



FIG 5

PERITONEAL NEOPLASM (ENDOTHELIOMA).



PERITONEAL NEOPLASM (ENDOTHELIOMA).

33. Two Cases of Peritoneal Neoplasm (Endothelioma).

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(Plates III.-VI.*)

On the 23rd November, 1923, there was obtained for the Gardens a female Blue Wildebeest, or Brindled Gnu (*Gorgon taurinus*). It was noticed to have a somewhat enlarged abdomen, and the purchase was more eagerly made in the belief and hope that the animal was in a condition described euphemistically as an "interesting" one. The swelling continued to increase steadily but was accompanied by progressive weakness during the later months of 1925 and the first two of 1926. As the animal was in obvious distress and unfit for exhibition its death was decreed on March 4th, 1926.

At the autopsy it was clear that the abdominal swelling was fluid in nature and the cavity was, therefore, tapped prior to section, and 61½ litres (107 pints) of a clear, straw-coloured fluid were drawn off. This contained a few flakes of lymph which was not blood-tinged and did not clot spontaneously. A little fluid escaped in the tapping and a certain amount remained behind. The total amount was probably about 65 litres, or 114 pints.

On opening the abdomen the striking feature was the great omentum, which formed a large, pale, fleshy-looking sheet with some scattered petechial areas. The whole was from one to one and a half inches in thickness, presenting a finely granular, greyish-white, suety or waxy appearance on section, while the surface itself was nodular, many smaller nodules, like sessile papillomata, being aggregated to form larger masses or plaques of growth. On scraping the cut surface a milky juice was obtained. Macroscopically, if only a small portion was examined, a mass might be regarded as tuberculous, for it strongly resembles agglomerated tubercles. The microscope, however, reveals a picture fundamentally different from that of granulomatous or tuberculous tumour. The under surface of the diaphragm was studded with similar nodules, the majority being the size of a pea, some a little larger (Pl. III, fig. 1). There was nothing abnormal noticeable on the upper surface, and both lungs and pleura were normal, the thorax being nowhere invaded. The thymus almost covered the anterior surface of the heart, this organ showing no abnormality.

* For explanation of the Plates, see p. 518.

On the surface of the liver was a score or so of small nodules and the spleen was similarly covered in front, but there were none in the interior of either viscus. Though in some recorded cases there has been extension of the tumour, usually by metastasis, to involve the viscera, in this case they had escaped in spite of the length of time during which the growth had existed. Where structures other than the omentum, namely the liver, spleen, and diaphragm, were affected, the deposits were limited to the surface and accounted for by contiguous spread. The ovaries were normal and there were no signs of pregnancy. There were two small pendent cysts in the peritoneum which were diagnosed by Professor Leiper as *Cysticercus tenuicollis*.

Microscopical examination of sections made from the omental growth and that from the surface of the liver and spleen showed:—

Omentum.—The deeper part of the surface covering fatty areolar tissue is thickened and separated from the masses of tumour-cells proper by a faintly-staining, finely granular layer, as if the constituent cells had undergone hyaline or myxomatous degeneration and had become fused, the nuclei being no longer recognizable. Interspersed among these faintly-staining areas are scattered tumour-cells and occasional polymorphonuclear leucocytes. Similar areas are visible, though of smaller extent, in the more cellular and deeper parts of the tumour.

Towards the surface the cells are rounded or polygonal and show a considerable variation in size. Some are epithelioid, others are more cubical and irregular, but all seem to have nuclei rich in chromatin and cytoplasm abundant. Several contain two nuclei, and a few three or four, but nowhere is anything resembling giant-cells seen. In other parts the cells are more definitely flat and epithelial in character, often disposed in alveoli, the walls being formed of the weakly-staining hyaloid, or faintly fibrillar structures, poor in cells, but the cells when present have drawn-out spindle-shaped nuclei. In parts the cells are arranged cylindrically; in others the cylindrical or alveolar spaces are, as it were, lined with them, so that when such are cut transversely they closely resemble a section of a gland-duct. The strands of cells may join up and anastomose with others (Pl. IV. fig. 2).

Spleen.—In the growth attached to the spleen the cells are mostly of a large epithelial type and the alveolar disposition of them in some parts is very distinct. The walls of some are seen to be formed of thick trabeculae, faintly fibrillar and even hyaline in appearance, and reminiscent of cartilage but with sparse spindle-shaped or round cells in place of cartilage cells. Within the alveoli the cells show fine fibrillar processes, which constitute the sole intra-alveolar matrix. The growth, though attached to the surface, does not invade the spleen-pulp.

Liver.—In the tumour attached to the liver a condition closely resembling that just described is seen, but in addition there are blood-vessels cut at various angles, and in some of these the

endothelium may be noticed to consist of large cells, perhaps several layers in depth. At certain sites also these cells are arranged circularly; they appear compressed and their nuclei are elongated, the whole bearing considerable resemblance to nests of non-keratinized cells.

The liver itself is not invaded, but the parenchyma is separated from the mass of growth by a dense zone of fibrous tissue, except at one isolated spot in the section where penetration is taking place (Pl. IV. fig. 3; Pl. V. fig. 4).

When we come to analyse the histological picture, the strands of cells bounded by the fine stroma call to mind developing blood-vascular tissue, though the contained cells are epithelial in character in place of corpuscles. In parts this resemblance is further borne out by the presence of blood-corpuscles within the cellular walls themselves composed of one or more layers, as if the original endothelial lining had undergone definite proliferation. The condition mentioned already as resembling cell-nests may have resulted from the total obliteration of the lumen by this growth of the lining cells.

The alveoli, which may be distended or filled-in lymph-spaces, may contain epithelial cells with no visible stroma at all; or processes from the cells produce a fibrillar stroma-like appearance; while, elsewhere again, the walls are composed of a dense fibrous tissue with only a few compressed cells.

In fact, different parts of the tumour and even of a small section of it show by no means a uniform picture. In some there are aggregated groups of cells, flat, cubical, or polygonal, giving the impression of being inlaid in a connective-tissue stroma. The growth thrusts itself into lymph-spaces to produce a definite alveolar disposition. At other sites the appearance approximates more to that of a sarcoma, and we see between the cells a fibrillar stroma; at others, again, the cells have processes which communicate with those of adjacent cells of their own kind or with neighbouring fibroblastic cells. Yet again we may see strands of epithelial cells bordered by large endothelium-like cells, the processes of the latter appearing to join up with fibres of the connective-tissue stroma.

As already mentioned, the cells may be cubical rather than spherical, and line an alveolus rather than fill it. Such, on transverse section, recalls an adenoma; or, by compression and obliteration of the space, a "cell-nest" appearance results.

The second case was of a simpler nature in that there was not such a variation of arrangement in the different parts of the growth as occurred in the Gnu. Probably the growth had not been developing so long: the animal was a small one, and death was due, not so much to the growth directly, as to an abscess of the face which invaded the brain.

This animal was a female Hamster (*Cricetus frumentarius*) which had been in the Gardens for more than two years. The findings at the autopsy were most interesting.

There was an abscess on the right side of the face extending backwards and upwards beneath the orbit and passing through the sph-nomaxillary fissure of the brain, with thrombosis of the ophthalmic veins and extension along the optic nerve and the second division of the fifth cranial nerve. The abscess proved on examination to have arisen from a Streptothrix infection.

The left lung presented minute white deposits, just visible to the naked eye and situated in the lower lobe. The right lung was, to all appearances, normal.

The abdominal cavity contained 120 c.c. of bloody fluid. When this had been withdrawn, there was seen to be a flat velvety growth involving the peritoneum, the upper part of the anterior surface of the bladder, the mesentery, the surface of the liver, part of the spleen, and the under surface of the diaphragm; there were also small deposits on the kidneys, mainly at the lower pole of the left, and also on the broad ligament.

The growth consisted, microscopically, of typical large endothelium-like cells with foamy protoplasm and processes forming small spaces in which was a granular and fibrinous debris, the residue of blood-destruction. In many parts the cells are of a syncytial character, and are sometimes arranged in acinar form enclosed by a fibrous stroma. In other parts the vacuolation has proceeded still further, and adjacent vacuoles have coalesced to constitute spaces of considerable size into which hæmorrhage has taken place. In the case of the liver these cells are seen to be closely applied to the surface of the organ, but nowhere do they seem to have penetrated it. In fact, in some situations the appearance macroscopically was as if the growth had been laid on, like a carpet, and it could be almost peeled off without damage to the liver beneath. Elsewhere, though there is no actual infiltration or penetration of the liver tissue, there is seen in sections a definite thin strand of fibrous tissue between the tumour cells and the hepatic tissue; the two are indeed united by this fibrous band and cannot be mechanically separated (Pl. V. fig. 5).

In the lung, however, these endothelial cells are arranged in small masses or groups, and by suitable staining are seen to lie within vessels. In this organ the cells appear more as solid plugs, though the characters of the individual cells are the same as those seen on the surfaces of the affected abdominal viscera. The growth seems, therefore, to have been transported to the lung by embolism. It is strange that the involvement of the lungs was not more general in this case, but against the probability of direct extension are the facts that the left lung was the one involved, though the growth was rather more on the right side of the liver, that the upper surface of the diaphragm showed no growth at all, and that the cells of the growth in the lung were intravascular (Pl. VI. fig. 6).

To name a tumour correctly may be a matter of much difficulty. In many the character and relative disposition of the several

components are sufficiently clear to enable us to state their origin. Others, on the contrary, have no characteristic arrangement, the constituent elements do not resemble any of the normal tissues, and, as Professor MacCallum states:—"Every unusual tumour which lacks characters that will permit its ready recognition stands an excellent chance of being labelled 'endothelioma' and relegated to oblivion." This is, perhaps, one of several reasons for denominating the growth which is the subject of this paper an endothelioma.

There is not yet any definite proof that a tumour *does* (presumably it *can*) arise from endothelium, and the diagnosis is often made not so much on positive as on negative grounds of exclusion. Probably, as the matter comes to be more minutely studied some of those tumours now pigeon-holed as endotheliomata will be removed from that rather dustbin category and placed among the carcinomata or sarcomata. Any tumour may in its progress invade lymph-channels and spaces, and the very presence of such foreign cells may stimulate the lining cells of the vessel or sinus to proliferation, even to actual obliteration of the lumen, but this is quite a different thing from the participation of the lining cells in the actual tumour-growth.

What are we then to understand by the term Endothelioma? On the analogy with the usual rules of the nomenclature of tumours the answer should be easy—a growth arising from and composed of endothelial cells, and by endothelial cells we imply those lining blood- and lymph-vessels and the cerebrospinal spaces. Are we to include also those which line the body-cavities, the pleura, and the peritoneum? One authority holds that these are of hypoblastic and epiblastic origin and are therefore epithelial, and the tumours having their origin from such cells must be epithelial tumours, like carcinomata. Another states that the close resemblance between endothelial and epithelial cells, which he consequently names "epitheloid," has led and does lead frequently to "confusion between endothelioma, a variety of sarcoma, and carcinoma."

If we seek for light by Adami's embryological basis of classification, the atmosphere at first appears to clarify, but the mist again begins to gather. A growth deriving from what is called "rind" tissue is a lepidic tumour, such, for example, as carcinomata or those which have their origin from the endothelium of blood- or lymph-vessels. The lining of the peritoneum, though in a sense a "rind" tissue, is itself derived from "pulp" tissue, and tumours originating from this are therefore designated secondary or transitional lepidomata, to distinguish them from carcinomata, or primary lepidomata. It would seem, then, that all we have to do is to see whether the cells of the growth are cells resembling endothelium, and the diagnosis is made. But, though the constituent cells *may* retain the simple character of lining cells, they may also, as they do in parts of the first tumour, revert to the more primitive characters of their pulp-tissue origin,

and instead of epithelial cells we have spindle-shapes and the resultant growth, or that part of it at least, comes to resemble sarcomata or malignant connective-tissue tumours, and we are back in the maze again.

When we bear in mind the fact that there are blood-vessels, lymph-vessels, and lymph-spaces with their lining endothelium in the omentum, as well as the cells lining the membrane itself, and that the tumour may arise in one or the other, it is obvious that the resulting growth may be a true endothelioma or a transitional lepidoma, or a mixture of the two; and I am not convinced that the last is so rare as many think, and certainly, if this is so, we have reason for the variability of the picture exhibited in stained sections from different parts of the same tumour. This variability has led authors to interpret their findings differently, and, according to the several views as to the character and origin of the growth, so have they varied in their terminology and nomenclature. Thus:—(1) Tumours showing on section groups of parenchymatous cells arranged in an alveolar manner in a fibrous stroma, as in parts of the tumour in the case described as the text of this communication, and arising in situations where there is no "epithelium" in the strict sense, cannot justly claim to be classed as carcinomata, or malignant epithelial growths. They have consequently in many cases been designated *alveolar sarcomata*. (2) It is held by some writers that if, as in the case of the pleura or the peritoneum, these tumours arise from the serosa cells, or more correctly the lining cells of the serous membranes, they are epithelial in origin, and are therefore *carcinomata*. (3) Others, again, boldly cut the Gordian knot by assuming that the growths arise, not from the lining cells of the membrane, but from the endothelium of the blood- or lymph-vessels, and they regard these tumours in consequence as true *endotheliomata*. There is only one link missing from the chain, but it is an important one—namely the definite origin of tumours from such a source has not been proved to occur. (4) These growths have also been considered as taking origin from the cells outside the vessels, and hence are called *peritheliomata*, in which there are sarcoma-like elements disposed extravascularly. This, however, is countered by the view that their origin is in reality the endothelial lining of the perivascular lymphatics; if this is so, the term "perithelioma" should lapse. (5) Owing to the cells of the tumour forming solid columns or cylinders of cells, and these having an epithelial character, such tumours have been denominatd *cylindromata*, and a variety of carcinoma. (6) Aschoff and, prior to him, Schmaus definitely class them as *sarcomata*, as they belong anatomically and genetically to the connective tissues or, rather, mesoblastic tissues; but owing to their resemblance to epithelial growths and to the predominant character of the cell-picture, they are named *endothelial cancer* by the former, *spurious epithelioma* by the latter, in contradistinction to true epithelioma from epidermal tissues. Aschoff

states, in another place, that some of the endothelial tumours conform so closely to the epithelial type that they cannot be distinguished from true carcinomata "unless we succeed in determining the origin after making serial sections, and not even then in all cases," thus begging the whole question. (7) Another name bestowed upon "endothelial cancer" of the serous membranes is *lymphangitis carcinomatodes*, because they often show a cancer-like structure with nests embedded in the fibrous stroma and strands of large epithelium-like cells; or they may consist of a fibrous but richly cellular tissue in which are groups of cells of endothelial character, or reversions of them consisting partly of the covering cells of the serosa and partly of the endothelial cells of the lymph-vessels and spaces. (8) Ribbert, leaving the question of origin undecided, denominated these tumours *cœlomic cancers*.

Gathering up the threads of what has been stated on this complicated question, we may say that the character and arrangement of the cells in this tumour are such that, judging from a study of the cellular morphology, the nature and origin of them cannot at present be determined beyond dispute. They may, and probably do, arise from the serosa lining cells; they may also be derived from the endothelium of the underlying lymphatic vessels or spaces. It does not help much to aver that possibly both occur and that in time we shall be able to distinguish between them. In the first of our two cases the former would appear to predominate at least, for there were no metastases found anywhere, and, as regards adjacent organs, the liver and spleen, the growth was limited to the surface. In the second, the fact of embolic foci being found in the lung points to invasion of blood- or lymphatic vessels rather than to derivation from vascular endothelium because of the widespread involvement of the surfaces of viscera without dissemination in the interior of them. According to V. Ball, tumours of the peritoneum such as this have been noted especially in the Horse; Cadéac and Roquet have recorded an analogous growth of the arachnoid in the Dog, and Herbert Fox mentions one arising from the pleura in a Clouded Leopard at the Philadelphia Zoological Gardens.

Under the term endothelioma have been included certain carcinoma-like growths originating in serous cavities; certain diffuse tumours of the meninges and other more solid circumscribed tumours of the dura or pia mater, compressing rather than infiltrating the brain. These are composed largely of spindle-cells, often with an admixture of fibrous tissue, and show concentric whorls of cells resembling cell-nests (Bowlby & Andrewes). They are usually benign. Finally, there is a miscellaneous group, innocent or, from a clinical aspect, merely of local malignancy, if one can use such a term, contrasting thus with carcinomata. Occasionally, however, they become truly malignant. If operation is undertaken for removal, they not unfrequently recur, but this recurrence is due in all probability to incomplete removal.

A final word as to the naming of these tumours of the serous membranes, in this case the peritoneum. The membrane itself is embryologically of mesodermal origin, and the "epithelium" lining it is thus a mesepithelium or, if arising from the living vascular cells, a mesendothelioma, and the better term, that is better than endothelioma for a tumour arising from such, to cover both, would be mesothelioma.

The photograph reproduced as fig. 1 was taken by Mr. F. W. Bond, the remainder by Mr. Martin Duncan from microscopical sections of the tissues. To both these gentlemen I wish to offer my thanks.

EXPLANATION OF THE PLATES.

Figs. 1-4 are of the Brindled Gnu (*Goryon taurinus*).

„ 5 & 6 are of the Hamster.

PLATE III.

Fig. 1. On the left is a portion of the great omentum covered by and infiltrated with endotheliomatous growth. On the right below, a section of the same, cut across to show the thickening of the omental sheet. On the right above, the under surface of the diaphragm covered with nodules of growth.

PLATE IV.

Fig. 2. Microscopical appearance of the growing edge of the tumour in the omentum. To the left is the main mass extending, on the right, into the omental tissue proper.

Fig. 3. Edge of the liver (right) showing Glisson's capsule thickened and infiltrated by the growing tumour (left).

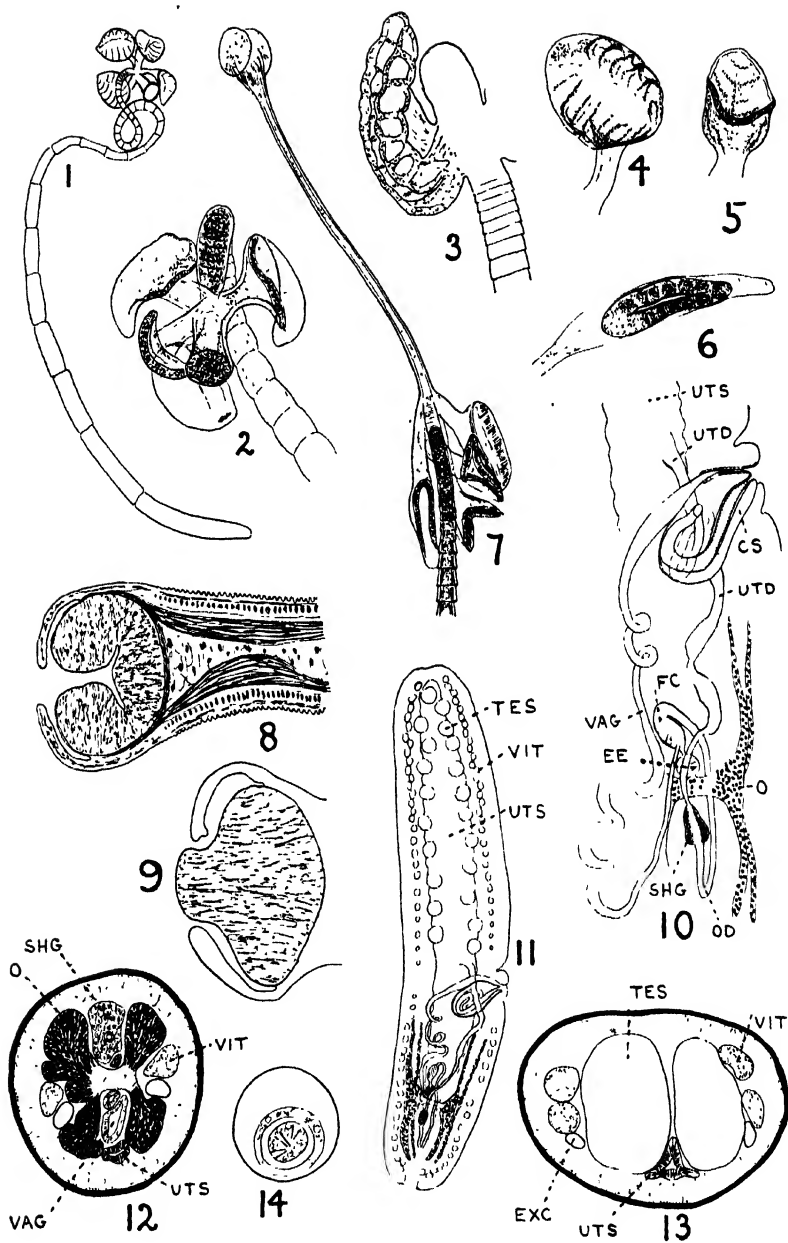
PLATE V.

Fig. 4. Edge of tumour growth showing marked thickening of the endothelium of a large blood-vessel and, just above this and to the right, a smaller vessel with its lumen practically obliterated by the endothelial hyperplasia. In other situations, by compression of these a definite cell-nest appearance is produced.

Fig. 5. Edge of the liver (upper part of section) covered by the thick carpet of endotheliomatous growth (below). Note that the hepatic tissue itself is not invaded.

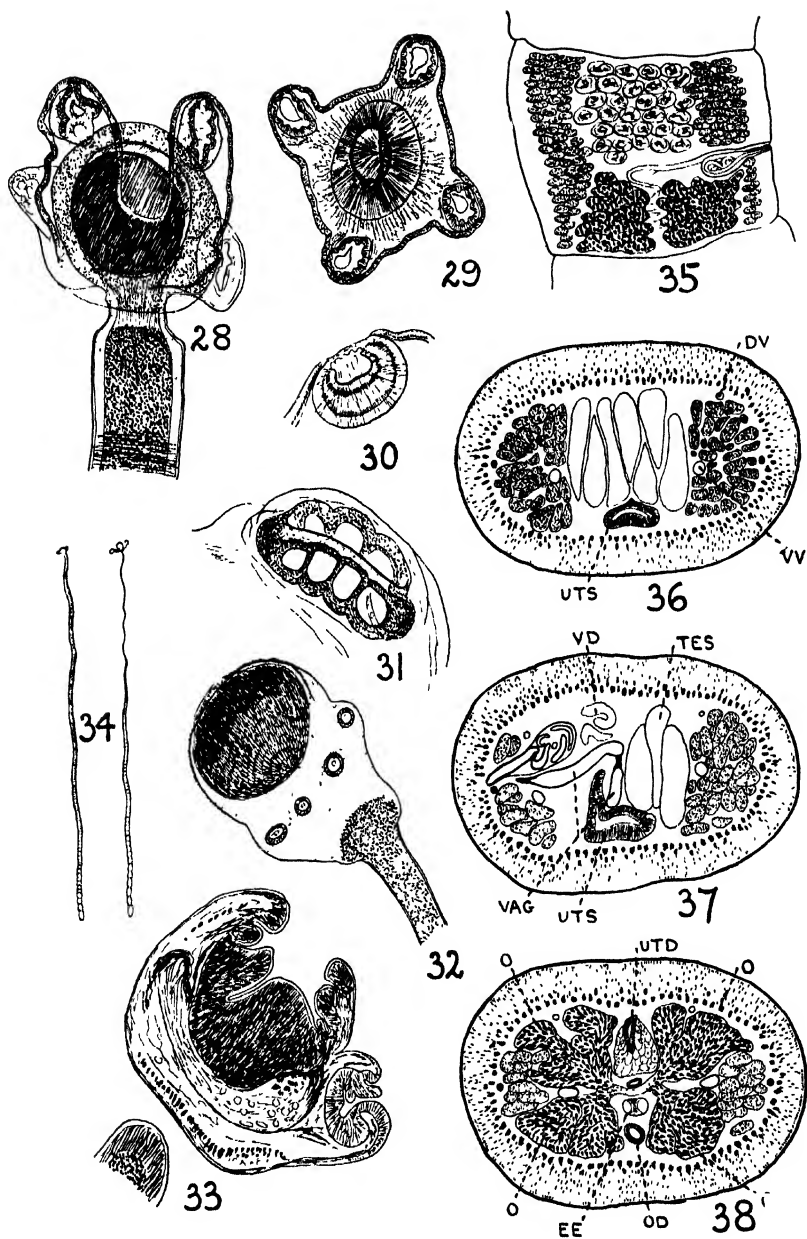
PLATE VI.

Fig. 6. Section of lung, showing the vessels in the walls of some of the alveoli distended and plugged by endotheliomatous cells. The air-passages themselves are free of growth.

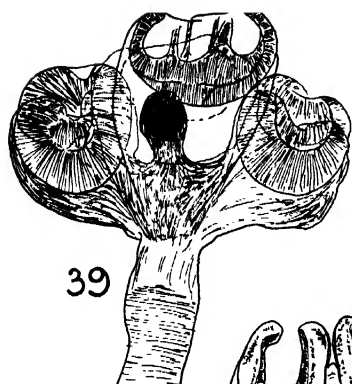


TETRAPHYLLIDEAN CESTODA.

2



TETRAPHYLLIDEAN CESTODA.



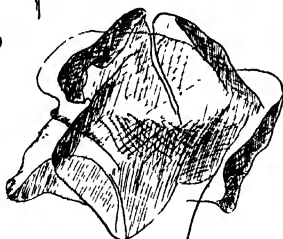
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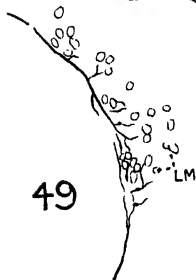
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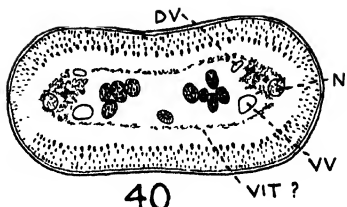
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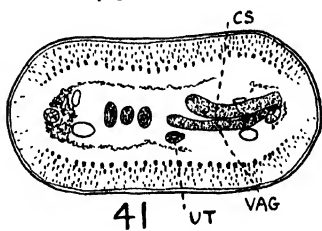
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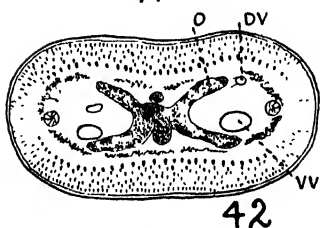
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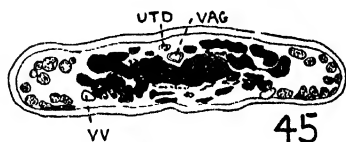
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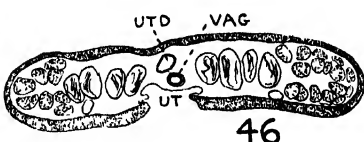
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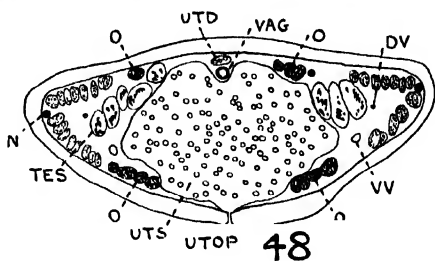
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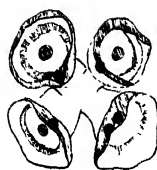
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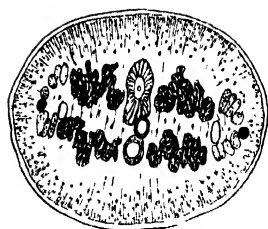
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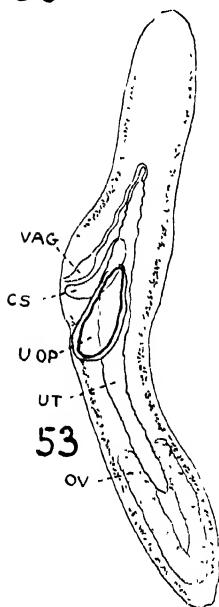
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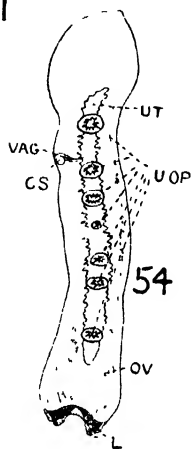
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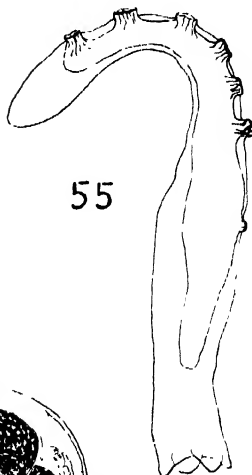
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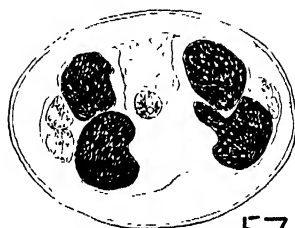
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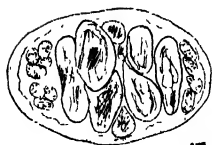
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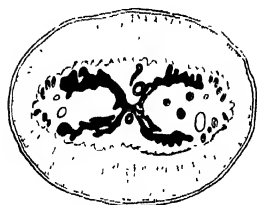
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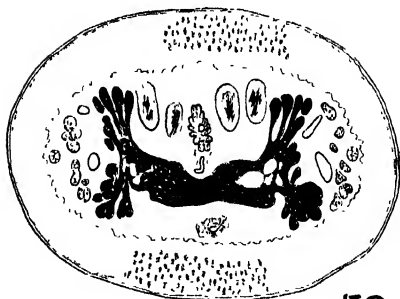
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34. A Revised Classification of the Tetraphyllidean Cestoda, with Descriptions of some Phyllobothriidæ from Plymouth. By W. N. F. WOODLAND, F.Z.S., Wellcome Bureau of Scientific Research, Endsleigh Gardens, London, W.C. 1.

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(Plates I.-V.*; Text-figure 1.)

During the autumn of 1925 I collected a large number of Cestodes from 450 fishes at Plymouth, and though most of my material necessarily consisted of forms already known, yet the careful examination of this enables me to add some information concerning the general characters of the Phyllobothriidæ and to supply reasons for revising the classification of the Tetraphyllidea as a whole. Before proceeding to discuss these subjects, however, I will report upon the examples of Phyllobothriidæ obtained by me at Plymouth, partly in order to describe one or two new species and to clear up some misapprehensions, but chiefly in order to elucidate the principal deep-seated general characters of this family. I may also here anticipate my final conclusions so far as to state that by the term Phyllobothriidæ I hereby designate both the unarmed and armed forms usually separated into two families—the Phyllobothriidæ and Onchobothriidæ—and that the Order Tetraphyllidea includes, from my standpoint, the three families of the Phyllobothriidæ, the Tetrarhynchidæ (usually regarded as a distinct Order, the Trypanorhyncha of Diesing), and the Proteocephalidæ.

PART I.—Phyllobothriidæ from Plymouth.

ECHENEIBOTHIUM MACULATUM, sp. n. (Pl. I. figs. 1-14.)

This small form is fairly common in *Raia maculata* at Plymouth, it having been found in 18 out of 47 fish examined. I will first briefly describe its structure, and subsequently indicate its chief features and affinities with other species.

Length of worm 8-15 mm., normally about 9 mm. Maximum breadth of terminal proglottids (before separation) about 0.232 mm. Number of segments in strobila varies between 29 and 70, normally about 50. The scolex is distinguished by a very prominent muscular rostellum (the so-called "myzorrhynchus") which, when most contracted (figs. 1, 2) is still conspicuous as a stout truncated pillar, and it can become extended to about six times its normal length (fig. 7). In longitudinal sections the extremity of the rostellum is seen to consist of a thick pad (fig. 9), covered with a circular fold of the

* For explanation of the Plates, see p. 547.

terminal subcuticula save for a small central opening. This pad can be retracted (fig. 8), and then resembles a sucker in form. Attached to the hind surface of the pad are strong retractor muscles, which are additional to the longitudinal and circular muscles in the subcuticula. The phyllides consist, in each case, of a proximal stalk and a distal expansion or bothridium. The stalk varies considerably in length, also the bothridium (0.249-0.348 mm.). The concave outer surface of the expanded bothridium is often subdivided into 15 or 17 loculi (areolae) by the temporary formation of ridges (costae) on each side (figs. 3, 4), but, under other conditions, these loculi are often entirely absent or at least invisible (fig. 2), and the edges of the bothridia may also become greatly thickened and the surface of the bothridium a nearly-closed cavity (fig. 6). Under other conditions the bothridia can contract and become crumpled to form a cabbage-like mass. The scolex therefore can undergo considerable changes of form.

The anterior end of the strobila practically shows no region of unsegmented neck.

The proglottids, unless strongly contracted, are all longer than broad except the most anterior, and, even when the strobila is contracted, the proglottids are still much longer than broad over the greater part of its length. The terminal segments, before separation, may be more than six times as long as broad, and anterior to these usually between four and five times as long. Terminal proglottids are shed from the hind end of the strobila in great quantity, and these isolated proglottids (fig. 11) are found in enormous numbers in the spiral valve intestine. They grow considerably after separation, and reach a maximum length of about 2.3 mm. and maximum breadth of nearly 0.5 mm. The genital apertures are irregularly alternate and are always situated a short distance behind the middle of the proglottid length, usually at about the beginning of the posterior third, but sometimes a little anterior to this.

The testes vary from 16-20 in number and lie in two rows, one on each side of the median axis (fig. 11), and vary in size according to development. When fully developed they occupy the greater part of the depth and breadth of the proglottid (fig. 13). The cirrus-sac is large and ovoid with a distinct though thin wall, measuring on an average about 0.186×0.106 mm. in isolated proglottids, extending in many cases over more than half the proglottid breadth and containing a much-coiled and very long cirrus. The outermost part of the unextruded cirrus (the basal portion of the extended cirrus) is thick-walled and probably muscular and bears minute spines internally, but this is soon succeeded by a much longer thin-walled much-coiled unarmed portion (the distal portion of the extruded organ). When fully extruded the cirrus exceeds in length the whole proglottis, and it can be seen that only the thick-walled basal part is armed.

The vagina opens immediately anterior to the opening of the cirrus-sac, and both openings are practically on the external surface, a sinus genitalis only being represented by a shallow depression. The vagina is very long and convoluted and dilated for a great part of its course, running dorsally to the uterus and ventrally to the uterine duct, and it opens posteriorly into the very conspicuous thick-walled ovoid fertilization chamber which is developed on the oviduct just anterior to the smaller spherical egg-ejector ("Schluck-apparat"), which last is situated on the anterior side of the median ovarian isthmus. From this fertilization chamber the oviduct goes posteriorly to the level of the hind end of the ovary, bends forward and develops a shell-gland, from which arises the uterine duct, which runs forward, crosses over the cirrus-sac and under the vagina, and opens into the median longitudinal egg-storing part of the uterus or uterine sac (fig. 10). The uterine sac is at first a simple elongated narrow sac, but it ultimately widens out and fills the whole proglottid, forming diverticula at its sides. I could detect no uterine aperture or apertures in my slide preparations, though when the living isolated proglottids were placed on slides they all immediately shed hundreds of eggs from one or more points presumably on the ventral surface.

The ovary takes the form of two dorsal and two ventral "horns," all four diverging from the ends of a central middle-piece or isthmus (fig. 10). Seen end-on the ovary would thus have the form of an X (fig. 12). In isolated proglottids the ovary extends over from one-quarter to one-third of the proglottid length. The vitellaria are over 100 in number and are located in two marginal strands, each strand consisting for the most part of two rows, and they extend from the anterior end of the proglottid to behind the ovary (fig. 11). Since there is no distinct cortical region of the parenchyma, the vitellaria, like the testes, must be regarded as medullary in position. The shed eggs (preserved in formalin) are spherical (fig. 14) and measure about 55 microns in external diameter. They possess two shells, an outer thin though tough shell and an inner thicker shell (about 22 microns in diameter). The contained embryos possessed the usual six hooks, about 11 microns long. When first deposited in the uterus the eggs are in clusters.

The excretory system consists of two main lateral channels, one on each side, situated at the periphery of the parenchymal zone and nearer the ventral than the dorsal side of the proglottid. These open at the posterior end of the free proglottid into a very distinct excretory bladder, which opens by a duct to the exterior in the middle line. I believe I could detect the two nerve trunks lying just external to the vitellaria, and midway between the dorsal and central rows. The longitudinal musculature consists of isolated fibres lying scattered in the region extending from underneath the cuticle to the innermost limit of the broad nuclear layer of the subcuticula (fig. 13). The only circular fibres present lie, in a thin layer, immediately under the cuticle and external to the outermost longitudinal fibres. There is no layer of circular fibres separating the longitudinal fibres from the parenchyma containing the genital organs.

Isolated proglottids, when fully ripe, are reduced to the condition of bags of eggs, most of the other organs having disintegrated.

The most noteworthy feature of the species just described is the prominent permanent rostellum. Other features worth remarking upon, as being characteristic of the family to which the species belongs, are the absence of a distinct internal layer of longitudinal muscles and the extension of the longitudinal muscle-fibres and bundles of fibres throughout the subcuticular layer, the position of the vagina dorsal to the uterine sac, and the quadripartite form of the ovary.

Of the twenty odd species of *Echeneibothrium* listed by Southwell (1925), only three can be regarded as possibly identical with the one I have described above. These are *E. affine* Olsson, 1866, *E. gracile* Zschokke, 1889, and *E. austrinum* Linton, 1924. *E. affine*, however, differs from my new species in having at least three transverse septa in the bothridium and in having a distinct neck, a cirrus armed over its entire length, and other smaller differences. *E. gracile* differs in apparently being devoid of a distinct permanent rostellum, in the terminal part of the cirrus being spiny, and in other small differences. *E. austrinum* differs in being longer and in having a short massive ovary (two oval lobes in surface view) and was found in South Africa. Doubtless these differences are small and yet they are sufficient to indicate for certain that we are not dealing with identical species, and I doubt the wisdom of Southwell's efforts to prove that the twenty odd *Echeneibothrium* species described can all be relegated to five valid species: it appears to me much more probable that all or

most of them are valid. I am confirmed in this view by the fact that Southwell regards as synonyms of *E. tumidulum* (a species itself "difficult to identify") the *E. affine* of Olsson (not unlike the species I have just described) and the *E. variabile* of van Beneden (described in part in the next section)—two species which are about as distinct as any two species of one genus can be. On the other hand, I do not believe that Southwell has gone half far enough in his restriction of the number of Phyllobothriid genera.

ECHENEIBOTHRIMUM VARIABILE van Beneden & E. ("DISCOBOTHRIMUM") FALLAX (van Beneden). (Pl. II. figs. 15-27; Pl. III. figs. 28-38.)

Though several zoologists (van Beneden, 1850, 1858; Olsson, 1866; Linton, 1889, and Beauchamp, 1905, for *E. variabile*; and Lönnberg, 1889, and Beauchamp, 1905, for *E. fallax*) have described the scolices and the main characteristics of the strobilæ of these two species, yet the facts that both Monticelli (1890) and Olsson (1893) considered these two species to be identical, while Lönnberg (1889) and Beauchamp (1905), on the other hand, considered that they belonged to distinct genera, show that a detailed comparison of these two species is essential. Braun (1900), without assigning any definite reasons, regarded the genus *Discobothrium* as a subgenus of *Echeneibothrium* and thereby implied that *E. variabile* and "*D.*" *fallax* are but two species of one genus, and this view is amply justified by the following comparison between the two species.

Body-Lengths and Proglottid Measurements

I possess seventeen specimens of *E. variabile* and nine of "*D.*" *fallax*, both species being found in *Raia clavata* and *R. maculata* at Plymouth, but *E. variabile* is mostly found in *R. clavata* and "*D.*" *fallax* mostly in *R. maculata*. The maximum length of body in both species is, in my material, about 70 mm. (in balsam), but the maximum breadth of the strobila is usually greater in "*D.*" *fallax* (in one 60 mm. unflattened spirit specimen 0.99 mm.) than in *E. variabile* (in one 60 mm. unflattened spirit specimen 0.64 mm.) and the anterior third of the strobila is always markedly more slender in mature *E. variabile* (0.11-0.19 mm. just behind the scolex in seven unflattened specimens) than in mature "*D.*" *fallax* (0.29-0.33 mm. in two unflattened specimens), and I can always distinguish the species externally by these differences of shape of the strobila, the slender anterior end of *E. variabile* being very characteristic (fig. 34). An unsegmented neck is usually absent in *E. variabile* but only occasionally so in "*D.*" *fallax*, and the posterior proglottids of the former species are usually longer in proportion to their breadth than in the latter species (cf. figs. 24 and 35), but neither of these two characters can be relied upon as trustworthy distinctions. A character which is more reliable is the nearly circular outline of transverse sections through mature and ripe proglottids of *E. variabile*, whereas the corresponding proglottids of "*D.*" *fallax* are nearly twice as broad as deep (cf. figs. 25-27 with 36-38).

The Scolices.

The differences of form and structure between the scolices of *E. variabile* and "*D.*" *fallax* are, though not very conspicuous, yet quite distinct, as may

be gathered from figures 15, 16, and 17 compared with figures 28 and 29 and the figures supplied by previous authors (*vide* Johnstone, 1906, and Beauchamp, 1905, *e. g.*). The rostellum of mature unflattened specimens of *E. variabile* is approximately spherical in form (cir. 0.664 in diameter in a 60 mm. specimen), often has an irregular outline at the apex due to protrusion through the large terminal aperture of the irregularly-shaped mass within (fig. 15), and has a base with a very irregular crenulated outline (fig. 16), marking the attachments of the retractor muscles (figured by Johnstone, 1910), and the bothridia arise well below the rostellum, are pedicelled and therefore more or less elongated and, though extremely variable in shape, usually show a number of loculi. In mature unflattened "*D.*" *fallax*, on the other hand, the rostellum is flatter in form (0.78 mm. broad by 0.38 mm. high in a 60 mm. specimen), this flat shape in part being due to the bothridia arising from the sides instead of from the base of the scolex, and has a more solid outline, the contained muscular mass being more spherical in form than in *E. variabile*, while the bothridia are always much shorter than in *E. variabile* and usually show but few indications of loculi. In young forms of *E. variabile* the rostellum is often very small compared with the bothridia and sometimes cylindrical in form (figs. 20, 22), the latter always being very evident, and these can thus be easily distinguished from the young forms of "*D.*" *fallax*, in which the rostellum is always large compared with the bothridia, which are merely represented by flat suckers (fig. 32). As figures 16-19 show, the bothridia of *E. variabile* can assume the most varied forms, even the hinged form (fig. 17) found in *E. flexile*. On the other hand, young forms of "*D.*" *fallax* (fig. 32) strongly resemble certain species of *Tylocephalum* (*T. ludificans*, *e. g.*), a genus which Southwell places in the Cyclophyllidea solely on account of the four suckers.

Internal Anatomy.

As regards the internal anatomy, distinctions between the two species are several in number and sharply defined. In transverse sections of *E. variabile* the ripe testes (20-27 in total number) rarely exceed four in number (fig. 25), whereas in "*D.*" *fallax* they (24-35 in total number) are about twice as numerous (fig. 36). The same remark applies to the vitellaria, those of "*D.*" *fallax* being two or three times as numerous as those of *E. variabile*. In *E. variabile* the cirrus-sac is relatively large (cir. 0.215 mm. long) and when fully expanded extends half-way across the proglottid (fig. 26), whereas in "*D.*" *fallax* it is relatively small (cir. 0.157 mm. long) and extends across at most one-third of the proglottid breadth (fig. 37). Finally, in *E. variabile* only one pair of large ventral excretory channels exists, lying immediately under the vitellarian strands towards the ventral side of the proglottid (figs. 25-27), whereas in "*D.*" *fallax* there are two pairs of excretory channels, the large ventral pair lying to the inner sides of the broad lateral masses of vitellaria and about midway in the proglottid depth, and the small dorsal pair lying dorsal to the vitellaria (figs. 36-38).

I may add that in both species a dorsal (posteriorly) uterine duct exists (the "oviduct" of Zschokke, 1889; the "ootype" or "primary uterus" of Haaswell, 1902-3; and the "uterine canal" of Johnstone, 1920) which opens into the uterine sac or uterus proper anterior to the ovary, that all my specimens were too young to show the ventral uterine opening, and that in both species the ovary assumes, in transverse section, the usual X-shape, with a dorsal shell-gland and a ventral egg-ejector. Also in both species the cirrus-sac and vagina pass dorsally to the lateral nerve (the reverse is the case in many Phyllobothriidae).

Though it is evident from the above description that the two species described are quite distinct, yet it is also evident that they are sufficiently closely related to be included in the same

genus, in which case the genus *Discobothrium* must disappear, so far as this species is concerned. Though Beauchamp says of the bothridium of "*D.*" *fallax* that "il ne présente aucune espèce d'alvéoles ou de replis transversaux" yet it is a fact that very distinct loculi are often to be found (fig. 31), and this fact removes the only objection to naming the species *Echeneibothrium fallax* (van Beneden, 1871). I may also mention that although a spiny covering of the rostellum (apart from the terminal "os") is quite evident in one of my young specimens of *E. fallax* (fig. 32) yet I cannot confirm Beauchamp's statement that it occurs in mature worms.

ECHENEIBOTHRIUM JULIEVANSIUM, sp. n. (Pl. IV. figs. 39-42.)

In 1889 Linton figured the scolex of a species of *Echeneibothrium* from *Raia batis* which he regarded as probably an aberrant form of *E. variabile*, and Johnstone (1906) likewise figured a somewhat similar form from *R. erinacea* which he also referred to *E. variabile*. I have also found a single immature worm in *Raia maculata*, the scolex of which somewhat resembles those figured by Linton and Johnstone, but transverse sections through the proglottids (even though immature) prove that the worm belongs to a distinct species.

This worm measures about 55 mm. in balsam, with a maximum breadth of 0.7 mm. The anterior half of the strobila is very slender (average breadth of 0.1 mm.), and in this respect it resembles the strobila of *E. variabile*. On the other hand, the immature proglottids are all much broader than long (e. g. the eighth segment in front of the terminal measures 0.58×0.19 mm.), except the bluntly-pointed last or terminal segment (which is only very little longer than broad, measuring 0.41×0.36 mm.), and this is very unlike the proglottids of immature or mature *E. variabile*.

The scolex is of the form shown in fig. 39. In balsam and slightly flattened, each phyllidium consists of a distinct thick pedicel which carries a thick-walled sucker-like bothridium measuring about 0.5 mm. in breadth. The walls of the bothridium show distinct traces of septa and therefore loculi, though they are few in number. The rostellum is, in my specimen, very small (0.24 mm. long and 0.17 mm. broad) and contains a large cavity with a terminal os. The unsegmented neck is so short as to be practically absent.

As I have already mentioned, the posterior proglottids of this worm are all immature; nevertheless it can be seen that the general arrangement of the organs is like that of other Phyllobothriidæ. The genital openings open marginally in the hind third of the proglottid length and are irregularly alternate. The testes are about thirty-two to forty in number (except in the terminal segment in which there are only about twenty-four) and are mostly disposed in two fields. The vitellaria are very undeveloped individually but their general distribution is normal, though, in transverse sections (figs. 40, 41), the two lateral masses of vitellaria appear to be joined across the medulla, dorsally and ventrally, by cords of similar embryonic cells (cf. Cohn's *Prosobothrium armigerum* from *Squalus acanthias*: vide infra). It is probable, however, that this annular arrangement of the vitellaria disappears in mature proglottids and only represents a vestige of the ancestral condition of these forms (vide Part II.).

These transverse sections also reveal the fact that two pairs of excretory channels exist—a fact sufficient to disprove the identity of this species with *E. variabile*. Another notable fact is that, as in *E. variabile* and *E. fallax*, the cirrus-sac and vagina pass dorsally to the lateral nerve (fig. 41). The ovary is X-shaped as usual.

This species is evidently quite distinct from the *E. dubium* of van Beneden, examples of which only consist of about twenty proglottids, the last of which is about one-third the length of the entire strobila. In *E. dubium* also the genital apertures are situated at about the middle of the proglottid length, and not behind, as in the present species.

SCYPHOPHYLLIDIUM GIGANTEUM (*Anthobothrium giganteum*
van Beneden, 1858), gen. n. (Pl. IV. figs. 43, 44.)

I discovered a single specimen of this species in the spiral valve intestine of *Galeus vulgaris* Flem. at Plymouth, associated with two specimens of *Anthobothrium cornucopia*.

The worm, flattened and mounted in balsam, measured roughly about 95 mm., but since an unknown number of the end proglottids have become detached and those proglottids which remain are very immature, it is impossible to guess as to its length in life when the worm was entire, but it must have been considerable. Van Beneden states that his specimens of *Anthobothrium gigantea* (a species with which I believe my species is identical) attained a length of 15 cm. and a maximum breadth behind of 2-3 mm.

The scolex of my specimen measured (in balsam) 1.19 mm. in breadth, and the individual "bothridia" about half this breadth. The "bothridia" (figs. 43, 44) are globose structures ("resemblent à des ventouses de ténia péculées"—van Beneden), with fairly thick walls, deep cavities, and irregularly-shaped slit-like openings. They appear to be practically sessile, though doubtless their basal attachments are capable of extension. I could detect no trace of loculi, and it is very doubtful if such exist in connection with such limited areas of wall. Though I was unable to cut horizontal sections across these "bothridia" I think I am justified in assuming that loculi are absent. A rostellum is absent and I could detect no spines. The unsegmented neck in my flattened specimen is very long, exceeding 30 mm.

The genital openings are situated in the anterior third of the proglottid length and are irregularly alternate. The proglottids are all broader than long in my specimen, the most posterior measuring (flattened) 1.57 × 0.78 mm. In surface view the very young proglottids appear to be of the normal Phyllobothriid type, and transverse sections confirm this. Since all my proglottids were artificially flattened before cutting I am unable to provide correct drawings and will merely record that the ovary is, as usual, X-shaped, that two pairs of excretory canals are present, and that the cirrus-sac and vagina lie ventrally to the lateral nerve (i. e. the opposite condition to that found in the three preceding species). The vitellaria were almost entirely undeveloped, but I believe they have the typical Phyllobothriid arrangement.

The above species was first briefly described by van Beneden and, so far as I know, it has not been redescribed. Van Beneden assigned it to the genus *Anthobothrium*, though he admitted that the bothridia have practically taken on the form of suckers. Because of the presence of these typical suckers I was at first inclined to refer the species to Cohn's genus *Prosobothrium* (*P. armigerum* found in the stomach of *Squalus acanthias*), but *P. armigerum* is not a typical Phyllobothriid*,

* Southwell (1925, p. 129) says that "the anatomy of *P. armigerum* is exactly similar to that of typical species in the Order Tetraphyllidea, but, as it apparently possesses four suckers instead of four bothridia, it appears that *P. armigerum* Cohn should be referred to the Order Cyclophyllidea, emended, and to the sub-Order Multivittellata." I am unable to agree with either the statement or the suggestion.

since it possesses a unilaminar ovary (*i. e.* not X-shaped in transverse sections but one-layered, as in Proteocephalidæ) and vitellaria arranged, in transverse sections, in a complete circle surrounding all the other organs except the lateral nerves (*cf.* *Echeneibothrium julievansium* above). It is also impossible, according to present methods of classification, to refer the species to Mola's genera *Aocobothrium* and *Cyatocotyle*, because the bothridia of these genera are cylindrical and the vitellaria form a circle round the other organs in the horizontal plane of the proglottid, and other features of the internal anatomy appear to be unknown. The only alternative, therefore, is to create a new genus to receive Phyllobothriid species possessing a simple scolex with bothridia modified into suckers and devoid of a rostellum (thus distinguishing the genus from the various "Lecanicephalid" genera), and I propose the name *Scyphophyllidium*. The distinctions between this genus and Proteocephalid genera (all the individuals of which possess suckers) will be indicated below.

The five species described above form an interesting series illustrating the gradual modification of the entire phyllidium into a sucker, just as individual loculi become modified into suckers. In *Echeneibothrium maculatum* the phyllidium consists of a long pedicel and a large expanded bothridium with a surface usually subdivided into numerous loculi; in *E. variabile* the bothridia are more compact and the loculi fewer in number; in *E. julievansium* and *E. fallax* the bothridium has become cup-shaped, with only traces of loculi, and the pedicel is practically absent in the latter species, and in *Scyphophyllidium giganteum* the bothridium is completely sucker-like, the pedicel only remaining as an extensible base, as in Proteocephalida. This modification of the entire phyllidium into a sucker evidently affords no more justification for transferring *Scyphophyllidium* from the Tetraphyllidea to the Cyclophyllidea than does the similar modification of loculi into suckers, since the main organization of the worm remains Tetraphyllidean, and the same remark applies to the Proteocephalids. In other words, so long as these worms retain their marginal vitellaria and ventral uterine pores, the appearance of suckers—organs developed both orthogenetically and adventitiously in so many different groups of the animal kingdom—cannot justify their inclusion with worms possessing a concentrated median vitelline gland and devoid of uterine pores. Cestodes, like other animals, must be classified by the majority of their characters and not by a single very capricious character, however convenient, and it is impossible therefore to accept that part of Southwell's scheme of classification which is based on the assumption that if a worm possesses four suckers on its scolex it must, *ipso facto*, belong to the Cyclophyllidea, quite apart from the possibility that its organization may, in all other respects, be typically Phyllobothriid or Proteocephalid. Still less sympathy have we with Southwell's other proposal to erect a new Order of

Cestodes to include worms with a "head very variable in appearance," only negatively characterized as possessing neither four suckers, four bothridia, four proboscides, nor two bothria—the sole definition of the Order!!

. ANTHOBOTHRUM CORNUCOPIA van Beneden, 1850.
(Pl. IV. figs. 45, 46.)

I obtained two large fully-mature specimens and a number of free proglottids from *Galeus vulgaris*, one about 90 mm. long. This form was first briefly described by van Beneden and fully described by Zschokke (1889).

Zschokke described clearly the uterine duct (dorsal to the vagina) which opens into the uterine sac anterior to the ovary, the dorsal shell-gland, and ventral egg-ejector. The ovary in this species is not strictly X-shaped in transverse section, as fig. 45 shows, but is irregular in form, consisting of a broad median piece with numerous dorsal and ventral extensions. The X-form is, however, more evident in young proglottids. The uterine aperture is only to be found in free proglottids, and it and the uterus proper (fig. 46) are almost exactly of the "*Solenotania*" type described by Beddard (1913) in a *Proteocephalid*. In other words, the uterus proper arises as a narrow median tube which later spreads a little to each side of the median line, and then, instead of extending throughout the medulla by developing lateral diverticula, as in most Tetraphyllidea, unites its ventral wall along its entire length (i. e. from just in front of the ovary to near the anterior limit of the proglottid) with the ventral subcuticula (previously attenuated for the purpose) and opens to the exterior, thus liberating the eggs as fast as they arrive by the uterine duct. Thus the eggs are never stored in the uterus and the uterine aperture is not a mere dehiscence, as is sometimes supposed. So far as I can see in my sections, only two ventral excretory canals are present, dorsal canals being absent. Also the cirrus-sac and vagina pass ventrally to the lateral nerve, i. e. the nerve is dorsal. The vagina lies, as usual, dorsally to the uterine sac.

PHYLLOBOTHRUM LACTUCA van Beneden, 1850.

This species, although one of the most familiar of the Phyllobothriidæ, has, curiously enough, not yet been described in any detail from a European host. Van Beneden gave a very brief general description of its anatomy (his specimens were obtained from *Mustelus vulgaris*) and stated, among other things, that the proglottids become free and attain a length of from 12-15 mm. and breadth of 4-5 mm., and that the genital apertures are situated in the first quarter of the proglottid length. Southwell (1921) gave a general description of the anatomy of what he believes to be this species from *Galeocerdo tigrinus*, caught off Ceylon, and again in his recent monograph (1925) he repeats this description for specimens obtained from *Trygon kuhli* and *T. walga*, also obtained from Ceylon, and in this latter description (which I alone consider) he also states that there are "free" proglottids and that in attached segments the uterus always remains tubular and devoid of eggs. Both of these authors thus describe the ripe proglottids as being free, and van Beneden provides a figure. Yoshida (1917), on the other hand, describes very fully the anatomy of what is probably this species from *Cynias manazo* Bleeker, caught off Japan, and in his description

he emphasizes the fact that the terminal proglottids do not become free and that these posterior proglottids contain uteri distended with eggs which are discharged from the median ventral line. Since my specimens of this species, obtained from the same host as that from which van Beneden obtained his specimens, agree in all essentials with Yoshida's description, it appears to be almost certain that the free proglottids described by van Beneden were really those of *Calliobothrium verticillatum*, a species commonly found, together with *P. lactuca*, in *Mustelus vulgaris*.

My largest specimen measured when alive, though contracted, about 180 mm. and the scolices (four in number) from about 3-6 mm. in diameter, according to the state of contraction. In all other respects my specimens agree with Yoshida's excellent detailed description, but he has omitted to supply the information that the uterine duct, which runs forward dorsal to the vagina, turns ventrally, anterior to the ovary, and opens into the uterus proper (uterine sac), as is usual in these forms. In young segments the uterus shows no signs of connecting with the exterior nor does the ventral subcuticula show any attenuation. In segments with egg-containing uteri the uterus dips down (as seen in transverse sections) among the muscle bundles of the subcuticula, causing this region of the subcuticula to become very thin, and ultimately the ventral subcuticula splits along the middle line and its edges become confluent with the thin walls of the uterus, which afterwards split, liberating the eggs. The elongated uterine orifice cannot therefore be regarded as a mere dehiscence. The ovary is typically X-shaped in transverse section.

PHYLLOBOTHRIUM UNILATERALE Southwell, 1925.

(Pl. IV. figs. 47-49.)

Zschokke (1889) described the greater part of the anatomy of a Phyllobothriid from *Squatina angelus* which he regarded as an example of van Beneden's *Phyllobothrium thridax*, but, as Southwell (1925) points out, Zschokke's specimens differ from those of van Beneden in the anterior situation and unilateral disposition of the genital openings in the former. Southwell therefore proposes the new specific name *unilaterale*.

I obtained from *Squatina angelus* one specimen, apparently of this species, which measured when alive about 120 mm. in length. In view of Zschokke's nearly complete description of this worm I need only refer to certain features with which he has not dealt. The scolex of my specimen is shown in fig. 47. Accessory suckers were apparently absent. This worm has posterior gravid proglottids, nearly square in outline and which apparently do not become detached. One remarkable and very characteristic feature which at once strikes the eye in transverse sections is the presence of a very thin but very black line which separates usually on all sides the central region of the medulla occupied by the chief organs from the peripheral region of the cortex wholly occupied by the subcuticula and the longitudinal muscle bundles. This line is fibrillated (fig. 49), some of the fibres penetrating at right angles to the line into the subcuticula and running between the longitudinal muscle bundles. This line may represent a thin circular muscle-layer, but if so it is unusually darkly coloured, and I have not seen its like in other Phyllobothriidae. This line is distinctly interrupted in the mid-ventral region from the anterior end of the ovary to a short distance in front of the ovary, and this interruption undoubtedly marks the site of the uterine aperture which in my material is very narrow (fig. 48). The uterine duct is of the usual kind and opens into the uterine sac at the level of the cirrus-sac. The uterine sac is large and

occupies the whole centre of the medulla, is full of eggs in my material and oval in transverse section, and therefore not divided up into diverticula, as is the case in so many other species. The uterine sac ends posteriorly just under the anterior end of the ovary. The ovary is typically X-shaped. There are the usual two pairs of excretory canals, and the lateral nerves are dorsal to the cirrus-sac and vagina.

, *ORYGMATOBOTHRIMUM MUSTELI* (van Beneden, 1850).
(Pl. V. figs. 50-53.)

This species was first briefly described by van Beneden in 1850 under the name of *Anthobothrium musteli*. Van Beneden in all probability included under this name three distinct species: (1) the species described in detail by Yoshida in 1917 under the name of *Orygmatobothrium velamentum*, n. sp., from *Cynias manazo*; (2) the species fully described by Zschokke (1889) under the name of *Anthobothrium* (*Orygmatobothrium*) *musteli* from *Mustelus* spp.; and (3) a species identical with or similar to that described by Linton (1889) under the name of *Orygmatobothrium* (later *Crossobothrium*) *angustum* (from *Carcharias obscurus*) and by Yoshida (1917) under the name of *Crossobothrium angustum* Linton (from *Triakis scyllium*), and which is not identical with *O. musteli* as Southwell assumes. Of this last species I possess one example from *Mustelus vulgaris*. The first species—Yoshida's *O. velamentum*, sp. n.—is to be regarded as identical with van Beneden's *Anthobothrium musteli*, because not only do the description and two of the figures of the latter author tally with the very full description supplied by Yoshida, but more than forty examples of this worm, which I procured from *Mustelus vulgaris* at Plymouth, also accord, in every detail, with Yoshida's description. On the other hand, Zschokke's *Anthobothrium* (*Orygmatobothrium*) *musteli* differs conspicuously from Yoshida's species and van Beneden's description in having bothridia of very different shape, in the genital openings being situated behind the middle of the proglottid length instead of in front, in having two pairs of excretory vessels instead of one pair, and in other particulars, and I suggest that Zschokke's species shall be renamed *O. zschokkei*. Linton's *O. angustum* also differs in several minor features from Yoshida's *O. velamentum*, since Yoshida describes both species successively in the same paper. Since Yoshida has omitted to describe several important features in his account of the present species (*O. velamentum* becomes a synonym of *O. musteli*) I will supply the deficiency.

One feature, observable in transverse sections, which forms a sharp contrast with *Phyllobothrium unilaterale* is the entire absence of any line of demarcation between the "cortex" and the medulla (fig. 52), though the longitudinal muscle bundles are arranged in the same way. Another difference is that in *O. musteli* there is only one pair of excretory channels—the ventral pair—situated internal to the vitellaria and nearly midway in the proglottid depth, but slightly more ventral. And a third difference is that the lateral nerves run ventrally to the cirrus-sac and vagina. The dorsal shell-gland, ventral egg-ejector, and dorsal uterine duct (which opens into the uterine sac well behind the cirrus-sac) are all of the usual type. The uterus is only visible as a ventral narrow tube in proglottids which still adhere to the strobila and in

the free proglottids (which attain a maximum length of about 7 mm. and about 2 mm. in breadth) it only becomes very slightly broader and develops laterally-crenulated margins (indicative of potential sacculations) and very soon opens ventrally, first of all by a distinct circular pore, with thick margins (fig. 53), which later elongates until the uterus cavity is open to the exterior along the greater part of its length: in other words, it is a uterus of the "*Solenotenia*" type, previously noticed in *Anthobothrium cornucopia*. The eggs are ovoid in shape, indeed almost spherical, measuring about 29×27 microns (in formalin).

CALLIOBOTHRIUM VERTICILLATUM (Rudolphi, 1819)

van Beneden, 1850. (Pl. V. figs. 54, 55.)

This common species has been well described by Zschokke (1889) and later by Southwell (1925). I have procured numerous specimens from *Mustelus vulgaris* and have cut many transverse sections.

As Southwell describes, there are two pairs of excretory canals, but the cirrus-sac and vagina in my sections pass (as is usual) between the two canals of each side, the small dorsal vessel being dorsal and the large ventral vessel ventral to the sac and vagina. I may also mention that the sac and vagina pass ventrally to the lateral nerve. A voluminous X-shaped ovary exists, also the usual uterine duct opening into the uterine sac. The free proglottids (figs. 54, 55) are very similar in general appearance and size to those of *O. musteli* (both worms are commonly found together), but can easily be distinguished from these others by the presence at the hind end of the four lacinate lobes characteristic of *C. verticillatum*, by the small spherical cirrus-sac (cir. 0.13 mm. in diameter) and the direct course at right angles to the proglottid edge towards the middle of the proglottid of the vas deferens and the vagina (in *O. musteli* the cirrus-sac is very large—cir. 0.8 mm. in length—and elongated in form and reaches the middle line of the proglottid, and the vagina and vas deferens run anteriorly to a point in the middle line anterior to the uterus before turning posteriorly), and by the form of the uterine pore. In both *C. verticillatum* and *O. musteli* the uterus retains its tube-like form (not spreading all over the medulla as in many other species), but in the former species the uterus develops distinct funnel-like downgrowths (figs. 54, 55), which pierce the ventral subcuticula and open to the exterior (I have counted from one to seven in number according to the size of the proglottid), whereas in the latter species a similar single downgrowth (sometimes two) develops about midway in the uterus length (fig. 53), which then extends anteriorly and posteriorly until in the fully-ripe proglottid the uterus aperture is represented by a long slit coextensive with the uterus length (in fig. 53 the initial pore has commenced to elongate). The eggs are spherical, the outer shell measuring about 29 microns in diameter and the contained embryo about 20 microns, but these are measurements of eggs preserved in alcohol, consequently eggs in formalin would be larger.

ACANTHOBOTHRIUM CORONATUM van Beneden, 1850.

Zschokke (1889) has described the anatomy of this species in detail and I have only to make the following comments, based on preparations of numerous specimens (the largest about 120 mm. in length) obtained from *Scyllium catulus* Cuv. (*Scylliorhinus stellaris*).

The ovary is not strictly X-shaped in transverse section but consists of a central (i. e. lying midway between the dorsal and ventral surfaces) sheet of cells with dorsal and ventral lobes given off dorsally and ventrally: it may be regarded as a modification of the X-shape type in which the dorsal and ventral bifurcations of the ovary lamina have either coalesced or not separated. It

remains true, however, that the ovary substance reaches, on both sides, to both the dorsal and ventral limits of the medulla. The lateral nerve lies dorsal to the cirrus-sac and vagina. Southwell states that *A. coronatum* differs from *Onchobothrium pseudo-uncinatum* in having a dorsal uterine duct which opens into the ventral uterine sac at the level of the genital pores, the short "oviduct" in *O. pseudo-uncinatum*, on the other hand, being continuous with the posterior extremity of the uterus. This is not exactly the case, since, as my sections clearly show, *O. pseudo-uncinatum* only differs from *A. coronatum* in that the uterine duct is short and bends ventrally while in the anterior region of the ovary, to open into the uterine sac as usual, the portion of the uterine sac posterior to this opening being short. The arrangement is otherwise identical in both species. There is no layer of circular muscles separating the longitudinal muscle bundles from the medulla.

ACANTHOBOTHRUM DUJARDINII van Beneden, 1850.

(Pl. V. figs. 56, 57.)

I have obtained numerous specimens from *Raia maculata*. This minute species has been briefly described by Linton (1908, under the name of *A. brevisseime*) and by Southwell (1925), and I will add some particulars in which my specimens differ from theirs.

The total lengths of my specimens (in balsam) vary between 1.4 mm. and 3.2 mm. The length of the terminal proglottid varies from 0.8 mm. to 1.0 mm. and in breadth from 177 microns to 282 microns. The lengths of the scolex range from 315 microns up to 713 microns and the lengths of the hooks from 109 microns to 175 microns. The number of proglottids varies between 4 and 8. These measurements and numbers, it will be noticed, differ considerably, both among the specimens themselves and also, especially those referring to the terminal proglottid, scolex, and hook, from those given by Southwell. The cirrus-sac is large (from 109×106 microns to 168×139 microns, these measurements differing largely from the 75×40 microns given by Southwell) and is situated about midway in the proglottid length, occupying in transverse sections nearly the whole of the medullary area. The ovary is, like the proglottid containing it, very elongated and narrow, but nevertheless shows, in transverse sections, the usual quadripartite form quite clearly (fig. 57). So far as I could observe them the longitudinal muscles and nerves are of the usual type. The uterus appeared to be undeveloped in all specimens.

ONCHOBOTHRUM PSEUDO-UNCINATUM (Rudolphi, 1819)

Beauchamp, 1905. (Pl. V. figs. 58, 59.)

I obtained several specimens of this worm from *Raia maculata*, which enable me to add some further details to Southwell's description of the anatomy.

In one large specimen (approaching 180 mm. in length or more) the last attached segment measured 4.3 mm. in length (flattened) and free segments attained a length of over 5 mm. (flattened). The lengths of the hooks surmounting each bothridium were about 113 microns, a length greater than those given by Southwell (70-90 microns). The unsegmented neck measured about 16 mm. long. The longitudinal muscles are, contrary to Southwell's statement, very well developed in mature proglottids (fig. 58), though it is true that in ripe proglottids with distended uteri the whole subcuticular region becomes reduced in thickness. Circular muscles at the periphery of the medulla are entirely absent. The lateral nerve runs dorsally to the cirrus-sac and vagina. The ovary when mature has the appearance shown in fig. 58 in transverse sections. In immature proglottids the ovary is of a typical X-form (fig. 59).

The vitellaria in mature proglottids form two narrow strips as usual, but, in many transverse sections of young segments, the vitellaria, in the region of the testes, form a more or less complete ring at the periphery of the medulla, surrounding all the other organs except the lateral nerves. This arrangement is noteworthy, and I shall remark upon it later. It will be remembered that a trace of this arrangement was to be seen in young proglottids of *Echeneibothrium julievansium* (vide supra).

A short uterine duct is present (vide under *A. coronatum*). The fully-developed uterus becomes crowded with eggs and fills the entire proglottid, the other organs degenerating. This is a sign that a definite uterine aperture (if such exists) is of very late development, and it is probable that the eggs are liberated by what is apparently mere dehiscence of the wall.

Summary of Part I.

1. Some general characters of the Phyllobothriidæ (sens. nov.), important from a classificatory standpoint, are: (a) the quadripartite form of ovary; (b) the position of the vagina dorsal to the uterine sac; (c) the distribution throughout the subcuticular layer of the fibres and bundles of fibres of the longitudinal muscle-layer, lying in a single peripheral zone; and (d) the vitellaria normally lie in two marginal strands but in the young proglottids of some species (e. g. *Echeneibothrium julievansium* and *Onchobothrium pseudo-uncinatum*) a concentric arrangement (in transverse section) is present, which is probably reminiscent of an ancestral condition.
2. Two new species of *Echeneibothrium* are described—*E. maculatum* and *E. julievansium*. A new genus—*Lyphphylidium*—is proposed to contain van Beneden's *Anthobothrium gigantea*, a Phyllobothriid species with a scolex bearing bothridia modified into true suckers, and a new species of *Orygmatobothrium* is instituted—*O. zschokkeri*.
3. *Echeneibothrium variabile* is definitely distinguished from "*Discobothrium fallax*" on anatomical grounds, and the latter renamed *Echeneibothrium fallax*.

PART II.—A Revision of the Classification of the Tetraphyllidea.

The General Characters of the Phyllobothriidæ sens. nov.

From an examination of the internal proglottid anatomy of the fourteen species of Phyllobothriidæ just referred to and from descriptions of other species by other authors, to be referred to later, I conclude that the following features are common to all true members of the family. The scolex, armed or unarmed, usually bears four phyllidea, i. e. more or less leaf-like expansions (bothridia) often borne on pedicels, but these in a few cases become modified into sucker-like organs indistinguishable from

those of the Proteocephalidæ (as in *Scyphophyllidium*, n. g.) and in other cases are absent or only represented by small so-called "accessory" suckers (some "Lecaniocephalid" forms). The genital apertures are marginal and usually irregularly alternate. The parenchyma is not divided by an internal layer of longitudinal muscle bundles into cortex and medulla, the longitudinal musculature being restricted to an undivided peripheral zone of fibres and bundles of fibres lying immediately internal to the thin circular muscle-layer underlying the cuticle and more or less co-extensive with the subcuticula. All the organs, except the lateral nerves, lie internal to the longitudinal muscle-layer. The vitellaria are disposed in two marginal strands (though traces of a concentric, *i. e.* annular in transverse sections, arrangement are visible in the immature proglottids of a few species). The ovary is typically quadripartite in form, consisting in each half of the proglottid of a dorsal and ventral layer and thus assuming an X-shaped form in transverse sections. In a few species, however, this plan is slightly modified, the dorsal and ventral laminæ fusing, though each bears dorsal and ventral projections occupying the whole depth of the medulla. The uterine organ is constantly divided into a small uterine duct lying dorsal to the vagina and a uterine sac (which varies greatly in size) lying ventral to the vagina, the duct usually opening into the sac anterior to the ovary. The uterine opening (or openings) is somewhat late in development and varies greatly in form, sometimes consisting of as many as seven or eight distinct ventral tubular canals, sometimes of only a single pore, sometimes of an elongated slit with distinct margins, and sometimes of a mere split resembling mechanical dehiscence. All available evidence points to the conclusion that the uterine openings are primarily preformed and not dehiscences due to an overfull uterus (*vide* Appendix). The vagina constantly lies dorsal to the uterus. The ripe proglottids frequently (but not always) become detached and free-living. All species parasitic in Elasmobranch fishes.

Characters apparently diagnostic of this family are the presence of phyllidea unassociated with proboscides, the single zone of longitudinal muscle bundles more or less co-extensive with the subcuticula, and the combination of the quadripartite ovary with a vagina dorsal to the uterus and with marginal vitellaria.

All accounts of the anatomy of the Phyllobothriidæ (especially those of Zschokke, Yoshida, and Haswell) show that the only distinction which can be made between the two old so-called families of the Phyllobothriidæ and Onchobothriidæ is the presence of hooks or spines on the scolices of the latter, but in my opinion this character, in view of the complete identity of general organization of all these forms, cannot serve as a family distinction, though the armed and unarmed forms can still be distinguished, if so desired, by being grouped into the original subfamilies of Phyllacanthinæ and Phyllobothrinæ (Carus, 1885), but this is a purely artificial separation.

The General Characters of the Tetrarhynchidæ Cobbold
(*Trypanorhyncha* Diesing).

The detailed anatomy of these forms is not very extensively known, but the few complete and accurate accounts available tend to show that the following features are characteristic of the entire family. The scolex normally bears four phyllideæ reduced to bothridia, either independent or fused in pairs, associated with four armed retractile proboscides, but in some cases (e.g. *Aporhynchus* Nybelin) the proboscides are absent and (should the internal anatomy of certain other species, at present included by Southwell in the "*Lecaniccephalidæ*," compel us to regard these as belonging to the present family) in others the bothridia also become modified into suckers. The genital apertures are similar to those in the *Phyllobothriidæ*. The longitudinal muscle-fibres and bundles of fibres, in the few species examined, instead of lying in a single thick subcuticular zone, become separated into a thin subcuticular layer of single fibres and an internal layer of large bundles situated internal to the subcuticula and intermingled with or lying immediately external to the vitellarian follicles, which latter cannot be regarded as "cortical." The internal layer of bundles, however, is not always present (I cannot detect it in *Tetrarhynchus tetrabothrium* e.g.) though usually so. The vitellaria are always concentric (in transverse sections of proglottids) and not marginal (i.e. linear) in arrangement and they usually lie, as we have just seen, in the same concentric zone as the longitudinal muscle-bundles. The ovary is quadripartite in form, as in the *Phyllobothriidæ*, and likewise the uterine duct, uterine sac, and uterine pore are similar in both families. The vagina lies ventral to the cirrus-sac and ventral to the uterine sac (an important character), as seen in transverse sections. Ripe proglottids often become detached from the strobila, as in *Phyllobothriidæ*. All or at least most species are, in the sexual stage, parasitic in Elasmobranch fishes.

Pintner (1913) states four other characters distinguishing the *Tetrarhynchidæ* from the *Phyllobothriidæ*, viz. that in the former family (1) the testes extend behind the ovary to the hind end of the proglottid (whereas in the latter family they are only to be found in front of the ovary); (2) the vas deferens runs from behind forwards and does not cross over the vagina (in *Phyllobothriidæ* the vas runs from in front backwards and crosses over the vagina); (3) the opening of the vagina is by the side of or behind the cirrus opening (in *Phyllobothriidæ* the vagina opening is in front of the cirrus); and (4) the genital atrium is muscular and sucker-like (in *Phyllobothriidæ* the atrium is not muscular). If these characters prove to be constant for all species they will be of value in defining the group, but they do not appear to me to be as "deep-seated" or at least as obvious as most of the characters which I have named.

The Tetrarhynchidæ thus, so far as is known *, differ from the Phyllobothriidæ only in usually possessing armed proboscides, a distinct internal layer of longitudinal muscle-bundles, concentrically-arranged vitellaria, a vagina situated ventrally to the uterus and cirrus-sac, and in some less conspicuous features.

On the other hand, the Tetrarhynchidæ, as all authors concede, fundamentally resemble the Phyllobothriidæ in all the essential features of organization and infest the same hosts, and I contend that since they are so obviously closely allied there is no justification for placing them in different Orders: they are evidently as closely (and probably more closely) related to each other as the various families into which the Pseudophyllideæ are subdivided. I therefore propose to revive van Beneden's well-founded procedure of placing the Tetrarhynchidæ in the Tetraphyllideæ along with the Phyllobothriidæ.

On the "Lecaniccephalidæ" Braun, 1900.

Southwell's emended definition of this family (Southwell, 1925) is solely based on the characters of the scolex, no attention having been paid to the internal structure of the proglottid save that indicated by the remarks that the genitalia are "as in Tetraphyllideæ, except, so far as is known, in two species in which the vitelline gland is single and posterior; genital pores ventral or lateral; uterine pores present or absent." In this supposed family the scolex is described as bearing four suckers and being made up of two portions: an anterior armed or unarmed retractile or non-retractile portion which may be entire or split up into tentacular processes, and a posterior portion similarly variable in form. If we divert attention from the scolex to the internal anatomy of the proglottid, we find that very little is known about this latter and that little can only be gathered by the careful study of the relatively few superficial descriptions which exist. All or most of the species contained in this so-called family are parasitic in Elasmobranch fishes, and this fact alone predisposes me, in the absence of sound anatomical evidence to the contrary, to regard them as of necessity belonging to one or other of the two families we have just attempted to define.

I will first comment on those "Lecaniccephalid" species which are probably to be placed in the Phyllobothriidæ. *Lecaniccephalum*

* I have myself only studied serial transverse sections of the common British species *Tetrarhynchus tetrabotheirus* and *Rhynchobothrius erinaceus*. My authorities for statements referring to the anatomy of other species and genera are Pintner, 1913, 1926; Linton, 1924, 1925; Johnstone, 1911; Yoshida, 1917; Nybelin, 1918; and Querner, 1925.

I cannot at present agree with Poche's (1925) conclusion that *Haplobothrium* is a primitive Tetrarhynchid, since it is possible that the true scolex of that form is an instance of parallel development and not indicative of genetic affinity (cf. the isolated evolution of such a form of scolex as that of *Polypocephalus* e. g.). Though we are very ignorant of the detailed organization of the so-called "Lecaniccephalidæ," it is probable that future enquiry will show that some of these forms, apparently altogether devoid of a Tetrarhynchid type of scolex, are much more closely related to the Tetrarhynchids than *Haplobothrium* with its ventral genital apertures.

peltatum Linton, *Cephalobothrium abruptum* Southwell, and *C. variabile* Southwell are probably all Phyllobothriids, as shown by the disposition of the longitudinal muscle-bundles in one subcuticular zone and the marginal vitellaria (and probably by Pintner's character (1), but the species differ as regards Pintner's characters (2) and (3)). This was Linton's opinion in the case of the first-named species. Likewise *Tylocephalum yorkei* Southwell is probably also a Phyllobothriid and for the same reasons (including Pintner's characters (1) and (3)). *Balanobothrium tenax* Hornell and *B. parvum* Southwell are also almost certainly Phyllobothriids, as shown by the single subcuticular zone of longitudinal muscle-bundles, the marginal vitellaria, and by the vagina being situated dorsally to the uterus (and by Pintner's characters (1), (2), (3)). Finally, the single zone of muscles and the marginal vitellaria also indicate that *Polypocephalus radiatus* Braun and *P. medusia* Linton and *Calycobothrium typicum* Southwell are Phyllobothriids, and Linton held this view regarding the species described by him.

It is true that the scolices of these species are very unlike the scolices of typical species of *Phyllobothrium*, *Anthobothrium*, *Echeneibothrium*, *Orymatobothrium*, and other ordinary Phyllobothriid genera, but Southwell himself is of opinion that the genus *Discobothrium* is "closely related" to *Echeneibothrium*, and there is very little difference between the scolex of *D. fallax* (*Echeneibothrium fallax*, vide supra and figs. 28, 32) and those of species of *Tylocephalum*.

I propose, therefore, subject to the species above-named being ultimately proved to be Phyllobothriids, that the genera *Lecanicephalum*, *Cephalobothrium*, *Balanobothrium*, *Polypocephalus*, and *Calycobothrium* be included in this family. I am unable to add the genus *Tylocephalum* because the type-species, whether *T. pingue* or *T. trygonis*, is insufficiently known anatomically.

Some other "Lecanicephalid" species, on the other hand, would, from the limited information available, appear to be Tetrarhynchid in organization. Thus in *Adelobothrium cetiobatidis* Shipley and *Tylocephalum marsupium* Linton the vitellaria are arranged concentrically, intermingling with a thick internal layer of longitudinal muscle-bundles, and the vagina is stated to be ventral to the cirrus-pouch (and ventral to the uterus? Southwell's fig. 195 contradicts his statement in the text). It is also Tetrarhynchid in Pintner's characters (2) and (3) but not in (1).

I may here remark upon the fact (stated by Southwell) that in this species and in *Tylocephalum dierama* Shipley & Hornell (which is probably also a Tetrarhynchid) the vitellaria are marginal in immature proglottids and that they only become concentric in ripe proglottids. This course of development is in marked contrast to the development of the vitellaria in *Echeneibothrium julievansium* and *Onchobothrium pseudo-uncinatum* (vide supra) in which a concentric arrangement ultimately becomes a marginal one.

I propose then, provisionally, that the genus *Adelobothrium* should be included in the family Tetrarhynchidae.

Of the remaining "Lecanicephalid" species, the anatomical information available compels us to await the results of further investigation before attempting their classification. Thus, Mola's *Phanobothrium monticellii* (from an unidentified Elasmobranch) is described as possessing a vagina ventral to the cirrus-sac (and apparently also ventral to the uterus-sac), an internal layer of longitudinal muscles and a ventral uterine opening—characters which would relegate it to the Tetrarhynchidae—but, on the other hand, the vitelline gland is described as a small body lying dorsal to the ovary—a most unusual feature if it be a fact. However, as just remarked, it is necessary to await further information concerning details of its internal anatomy before deciding on its appropriate systematic position, and I think Poche's bold procedure of placing this genus in the "Tæniinea" is certainly premature. Similarly, Shipley and Hornell's *Tylocephalum trygonis* and *T. uarnak* are described as possessing small bilobed vitelline glands, placed behind the ovary, and the same feature is apparently present in Linton's *Discocephalum pileatum*. If the facts be as stated, the vitelline glands in these species have evidently assumed a Cyclophyllidean form, but in the absence of corroborative evidence from the rest of their anatomy, this feature by itself provides no valid reason for regarding these species as Cyclophyllidean, since, although they also possess acetabula on their scolices, the rest of their organization is in all probability strictly Tetraphyllidean. Bothriocephalid anatomy also shows us great variations in the disposition of the vitellaria in that group, and in such a form as *Parabothrium bulbiferum* Nybelin, the vitellaria have almost assumed the disposition just described for the aberrant "Lecanicephalid" species just mentioned, being restricted to the posterior half of the proglottid and situated only on the ventral side of the medulla in two small patches lying in the region of and under the ovary (Nybelin, 1922; Woodland, 1927). Pending further enquiry into the anatomy of *Phanobothrium monticellii*, *Discocephalum pileatum*, and the aberrant species of *Tylocephalum* named, I fully agree with Poche's criticisms (1925, pp. 369, 370) of the statements of Linton and Southwell regarding the vitelline glands of the species described by them.

The great variety to be found in Bothriocephalid anatomy indeed prepares us for meeting with anomalous combinations of characters in some species which must be regarded as isolated survivors from the period during which Pseudophyllidea gave rise to Tetraphyllidea. Cohn's *Prosobothrium armigerum* (from *Squalus acanthias*) is an example. This form combines concentric vitellaria (a Tetrarhynchid character), with a unilaminar ovary (a Proteocephalid character), a single subcuticular zone of longitudinal muscles (Phyllobothriid) and a vagina dorsal to the uterus (Phyllobothriid and Proteocephalid character). Again,

Linton (1925) has described as a Proteocephalid a parasite which he calls *Ichthyotania adhaerens*, which is from Elasmobranch hosts—*Cestracion zygeta* and *Galeus glaucus*. If this Cestode be a Proteocephalid it is the first to be described from Elasmobranchs, so far as I know. Linton's justification for describing it as a Proteocephalid is the simple scolex with four suckers and a unilaminar ovary; on the other hand, the vitellaria are concentric—an unique feature in a Proteocephalid. It will be interesting to know whether the vagina is dorsal or ventral to the uterus in this form. Since I regard the concentric disposition of the vitellaria as a more important difference from other Proteocephalids than such characters as the one- or two-field disposition of the testes, or the presence or absence of spines on the scolex, I propose to rename Linton's species after its describer—*Lintoniella adhaerens* (Linton).

The General Characters of the Proteocephalidae.

In the Proteocephalidae, as is well known, the phylliden have become replaced by typical suckers, usually borne on protrusible lobes, often only apparent when protruded. The genital apertures are similar to those in the Phyllobothriidae and Tetrarhynchidae. The parenchyma is normally subdivided into two regions (cortex and medulla*) by an internal layer of longitudinal muscle bundles, but this is occasionally absent (cf. Phyllobothriidae), in which case the longitudinal musculature is situated wholly external to the nuclear layer of the subcuticula (in the Phyllobothriidae the bundles are in the subcuticula as well as external to it). The vitellaria are always disposed (save in *Lintoniella*, n. g., assuming that this is a Proteocephalid) in two marginal rows, but it is interesting to note that in some species the strands become very thick posteriorly and correspondingly attenuated anteriorly, and posteriorly spread somewhat towards the median line—a condition which, in conjunction with the scolex suckers, is, as Beddard first pointed out, perhaps prophetic of a Cyclophyllidean condition. The ovary is always unilaminar (in *Proteocephalus tigrinus* the lamina gives off dorsal and ventral projections, so resembling to some extent the ovary of some atypical Phyllobothriidae). The uterine organ is frequently divided into a uterine duct and a uterine sac, but in other cases the sac is continuous posteriorly with the oviduct. The uterus opens ventrally by preformed pores or more extensive longitudinal orifices. The vagina, although it may in some species be

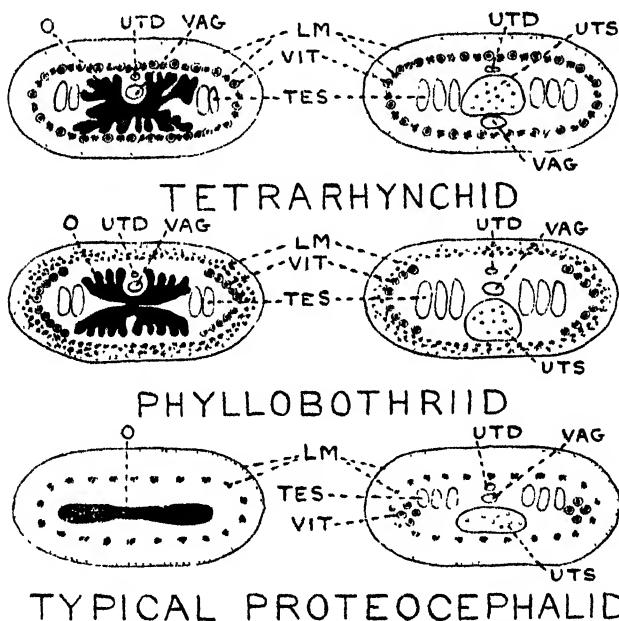
* Some authors wish to employ the innermost transverse (circular) layer of muscles, which often lies just internal to the internal longitudinal muscle-layer, as the line of separation between the "cortical" and "medullary" areas of the parenchyma, but this thin layer of circular muscles is no more stable than the layer of longitudinal muscles and certainly not so obvious. I am aware that the distinction between "cortical" and "medullary" is in many cases a futile one, but since the older authors lay great stress on this distinction, and utilized it as a family character, and since it is probably of real importance in some cases (instance the genera *Monticellia*, *Ephedrocephalus*, and *Mareypocephalus* in the Proteocephalidae), it is still necessary to recognize it.

situated ventrally to the cirrus-sac, always runs dorsally to the uterine sac. The natural separation of ripe proglottids from the strobila is only found to a very small extent and the original terminal segments are alone concerned. All species (except *Lintoniella*, from an Elasmobranch) found in freshwater Fishes, Amphibia and Reptilia.

The General Characters of the Tetraphyllidea.

Since those species which have been united in the so-called family of the Lecanicephalidæ possess no more tangible bond of

Text-figure 1.



Diagrams to illustrate the Distinctions, in Sections of Proglottids, between the three Families of the Tetraphyllidea.

union than a scolex "made up of two portions," each so variable in form as to exclude any idea of family affinity and, after all, only equivalent morphologically to subdivisions of the scolex proper, or to the rostellum and scolex of other Cestodes, it is evident that, until more substantial evidence of mutual affinity is adduced, they cannot be regarded as constituting a true morphological group, and I have, therefore, on most insufficient grounds due to the lack of detail with which these forms have been described, attempted to relegate the majority of them to one or

other of the older-established families. I have also shown reasons for believing that the so-called Order Trypanorhyncha cannot exist as a separate Order. Forms possessing bothridia, quadripartite ovaries, uterine pores and genitalia, which on the whole are universally admitted to be of the Tetraphyllidean plan, cannot stand apart from the Tetraphyllidea in the same sense that the Pseudophyllidea and Cyclophyllidea stand apart, and the only alternative is to revert to the original view of van Beneden that, despite their peculiar possession of proboscides, they form but one family of the Tetraphyllidea, fairly closely allied to the Phyllobothriidæ. In both these families the bothridia in certain species tend to assume the form of suckers, and in some cases actually become suckers, and the Proteocephalidæ only differ, as regards the scolex, from these other two families in that the bothridia in all cases have become suckers, borne usually on protrusible lobes.

The problem is, in advocating the inclusion of these three families in one Order, to find deep-seated characters common to all, which shall distinguish them from the other two Orders of Cestoda. Such characters are either very inadequately stated or not stated at all, in the definitions of these three Orders, which occur in current text-books and monographs. Apart from certain typical characters of the scolex (which are invaluable in classification, though, as I have attempted to show, this statement cannot always apply to the mere presence of suckers and certain minor features which often afford no guidance at all) the principal organ which affords grounds of distinction is the uterus. I will first state the general characters of the Tetraphyllidea, and afterwards the diagnostic characters which enable us to distinguish these forms from the Pseudophyllidea and Cyclophyllidea.

The general characters of the Tetraphyllidea are: the scolex may be armed or unarmed, and normally bears either four phyllidea only (with or without "accessory" suckers), four phyllidea associated with four proboscides, or four suckers only, and may or may not carry a rostellum (*i. e.*, a projection extending anterior to the phyllidea, proboscides, or suckers, which may contain a special musculature, and bear a terminal organ as well as accessory organs, or may simply be represented by an "apical" organ). In a few cases the scolex is apparently devoid of all appendages (phyllidea, proboscides, suckers), unless it be supposed that these have fused into a single structure (*Discocephalum*). The genital apertures are always marginal*. The ovary may be bilaminar (quadripartite) or unilaminar in transverse section. The vitellaria are always of the scattered type, *i. e.*, not concentrated into one small compact body. The uterus always originates as a narrow elongated canal running longitudinally in the middle line of the proglottid and may persist in

* *Tylocephalum narnak* Shipley & Hornell is stated to have ventral genital pores in young proglottids, but this apparently remarkable species, like its fellows, has not yet been described with the careful accuracy which it deserves.

this condition, but it normally becomes enlarged so as to occupy the greater part of the medulla and usually bears lateral diverticula. The uterus in the vast majority of, if not in all, cases opens on the ventral surface usually by one or more pores, but occasionally by longitudinal slits. It is doubtful if the eggs are ever liberated by mere dehiscence (*vide* Appendix) apart from a preformed opening or rudiment of opening. Ripe and mature proglottids frequently become detached individually from the end of the strobila. Parasitic in Fishes, Amphibia, and Reptilia.

The only partially diagnostic single characters, *i. e.*, characters which distinguish some of the species of this Order from all species belonging to the other two Orders, are the presence of phyllidea and proboscides, a quadripartite (X-shaped) ovary (the ovary in Pseudophyllidea is, so far as I know, always unilaminar though often curled up dorsally at its edges, and always unilaminar in Cyclophyllidea), and individually-detachable terminal segments*, but none of these characters is diagnostic of all Tetracyllidea as distinguished from the other two Orders, and it is therefore necessary to find a combination of characters which shall serve this purpose.

The only Pseudophyllidea which, as regards the proglottids, can possibly be confused with Tetracyllidea, are the Amphicotyliidae (*vide* Nybelin 1922), since these forms possess marginal genital pores, a median sac-like uterus (the uterus in the other family with marginal pores, the Triænophoridae, is a coiled tube), in some cases with lateral sacculations, and vitellaria either cortical and concentric or semi-concentric, or medullary and concentric (so resembling those in Tetrarhynchidae), or semi-concentric (*i. e.*, two marginal semi-circles, as in many Phyllobothriidae), or medullary and marginal (as in Proteocephalidae), or medullary and restricted to two small patches underlying the ovary (an approach to the Cyclophyllidean condition), and it is, perhaps, significant that some of these Amphicotyliidae infest freshwater Teleosts. These Amphicotyliidae, which probably represent the surviving remnant of the group which gave rise to both Tetracyllidea and Cyclophyllidea, very closely resemble Tetracyllidea in their general organization, and, in fact, the only character which enables us at once to distinguish them is the dibothriate scolex, and even this is absent in the case of some deformed scolices (*e. g.*, in *Parabothrium bulbiferum*). The only combination of characters then which enables us to distinguish all Tetracyllidea from all Pseudophyllidea is the presence of marginal pores and elongated saccular uteri, associated with a Tetracyllidean scolex. On the other hand, the Tetracyllidea can in the vast majority of cases be easily distinguished from all Cyclophyllidea by the presence of uterine pores or slits, and by the marginally- or concentrically-arranged dispersed vitellaria,

* In Pseudophyllidea it is stated that proglottids are detached in groups and not individually. I do not know whether this statement is valid for all segment-detaching Pseudophyllidea or not.

but, as we have seen, a very few Tetraphyllidean species are said to possess concentrated forms of vitelline glands, and likewise uterine pores have been stated to be absent in some cases, but these exceptions are so rare that they are of little importance. The diagnosis of the Order Tetraphyllidea then, in order that all, or at any rate the vast majority of, its members may be distinguished from all the members of the other two Orders, must be one expressing the combination of the characters just given, viz., a Tetraphyllidean scolex (see definition in general characters given above), marginal genital pores, longitudinally-elongated median saccular uteri, ventral uterine pores or slits or vestiges of such which appear as dehiscences, and dispersed, marginally- or concentrically-arranged, vitellaria.

Poche's section on the Cestoda in his elaborate and in many ways novel 'System der Platyhelminthes' (1925), affords an almost amusing contrast with the system of classification advocated by Southwell. Southwell bases his divisions almost entirely on the characters of the scolex, whereas Poche has so little respect for these characters in this connection that, despite their concentrated vitellaria, he unhesitatingly transfers the Tetrabothriidæ to the "Bothriocephalidæ" and, despite their scattered vitellaria and uterine pores, groups the Phyllobothriidæ (with the Proteocephalidæ, Lecanicephalidæ, and Polypocephalidæ) with the "Tæniinea" (Cyclophyllidæ). However, the feature about Poche's classification which now concerns us is the fact that when he treats of the Tetrarhynchidæ he retains his respect for the proboscidian type of scolex and, following tradition (no other reason is assigned), regards this family as an Order—the "Tetrarhynchiea"—distinct and separate from the "Phyllobothriinea," which latter group, as we have just seen, is placed as a suborder of the Cyclophyllidæ. I, on the contrary, for the reasons already given, maintain that the Tetrarhynchidæ are sufficiently closely allied to the Phyllobothriidæ to be regarded, with the Proteocephalidæ, as families of the same Order (Tetraphyllidæ). Poche further maintains Braun's family of the Lecanicephalidæ without attempting a definition, though it is based solely on relatively trivial scolex characters (the detailed proglottid anatomy being for the most part unknown), the importance of which, even when of ordinal value according to former investigators, he denies. I may add, in connection with Poche's remarks on Southwell's genus *Ilisha*, that this name must be deleted as applied to a Cestode because it has already been pre-occupied for a fish—*Ilisha* Gray 1846 (in Richardson's Ichth. China).

Summary of Part II.

1. A study of the internal anatomy of typical Phyllobothriidæ (the Phyllobothriidæ and Onchobothriidæ of other authors) and typical Tetrarhynchidæ shows that these two families only differ anatomically (i. e., apart from the scolex) in

that in the latter a separate internal layer of longitudinal muscles is present, the vitellaria have a concentric arrangement (instead of marginal), and the vagina lies ventrally to the uterine sac (not dorsally, as in Phyllobothriids). There is thus no justification for relegating the latter family to a distinct Order, and we therefore include both families (the Phyllobothriidæ and Tetrarhynchidæ) in the Order Tetraphyllidea, together with the Proteocephalidæ.

2. The family Proteocephalidæ only differs constantly (apart from the scolex) from both of the other two families in possessing a unilaminar (as distinguished from a quadripartite) ovary. The species recently described by Linton under the name of *Ichthyotœnia adhaerens*, and now renamed *Lintoniella adhaerens*, differs from all other Proteocephalids in having concentric vitellaria and in being found in Elasmobranchs, and possibly in other particulars.
3. Previous investigators have not appreciated at their full classificatory value the form of the ovary in transverse section and the position of the vagina relative to the uterine sac in the three families just named, since these characters, in conjunction with the distribution of the vitellaria and longitudinal muscles, will enable us, should subsequent enquiry prove them to be valid for the majority of species, to refer Tetraphyllidean species to their appropriate family with confidence. Southwell's remark (1925 a) that "in the absence of a head, it is frequently impossible to refer a Cestode worm to the Order to which it belongs," is thus, in all probability, unduly pessimistic, since serial transverse sections will enable us, in the vast majority of Tetraphyllidea and Pseudophyllidea, to refer any given proglottid not only to its Order, but to its appropriate family.
4. Braun's family Lecanicephalidæ (Linton's Gamobothriidæ) and Southwell's Order Heterophyllidea are both based solely on the presence or absence of certain scolex characters and are purely artificial groupings devoid of any standing. Until accurate complete anatomical descriptions of these forms are forthcoming, their correct allocation in any classificatory scheme must be a matter of conjecture only. It is evident that while the presence of two bothria, four phyllidea or four proboscides appear to afford a certain indication for the allocation of any particular species, the presence of four suckers is not a character of equal value, and the assumption that it is can only lead to dire confusion.
5. An attempt has been made to define more accurately the Order Tetraphyllidea, as distinguished from the other two Orders—Pseudophyllidea and Cyclophyllidea.

In conclusion, I wish to express my indebtedness to the Plymouth Marine Biological Station Table Committee of the British Association for the Advancement of Science for kind permission to occupy the Table during two months in the late summer of 1925, to Dr. E. J. Allen, F.R.S., F.Z.S., and the staff of the Plymouth Laboratory for much assistance in enabling me to procure Cestode material, and to Dr. H. A. Baylis for much friendly comment and criticism.

APPENDIX.

Note on preformed Uterine Pores in the Phyllobothriidæ.

There is no dispute concerning the preformed uterine pores of Proteocephalidæ and Tetrarhynchidæ, but Southwell (1925 *a*), following previous authors, questions their general occurrence in the Phyllobothriidæ, stating that "the presence of true uterine pores has only been established in about six species." The supposition that true uterine pores are generally absent in this group has long held sway and doubtless originated with the statements of Pintner and Braun. These authors called attention to the variable position of the pores in different proglottids, and attributed the slits which they admit do exist to the pressure of the filled uterus on the atrophied ventral parenchyma, but the variable position cannot discount the fact that the pores are, in many cases at least, due to active outpushings of the ventral uterine wall, nor can the atrophied parenchyma be attributed to egg-pressure, when this "atrophy" occurs previous to the filling of the uterus, as it certainly does in some cases. Nor can we ignore the fact that very few Phyllobothriid species have been properly examined in serial sections. Of the seven species (six genera) with developed uteri, so fully described by Zschokke, all possessed uterine openings (five other species described by him were immature), and of the four mature species described by Yoshida three possessed uterine openings (the five other species in his list either being immature or not described in detail), no pore being found in *Crossobothrium angustum*. Haswell was of opinion that in *Phyllobothrium vagans* the eggs were liberated by dehiscence. Dehiscence apparently also occurs, according to my observations, in *Echeneibothrium maculatum* and in *Onchobothrium pseudo-uncinatum* and, according to Linton, in *Thysanocephalum crispum*; on the other hand, I have observed true preformed (I include in this term obvious changes occurring in the parenchyma and musculature, previous to the filling of the uterus with eggs, which serve for the future uterine opening) pores or gapes in most of the species described by Zschokke and also in *Phyllobothrium unilaterale* (Zschokke's *P. thridax*), *Orygmatobothrium musteli*, and *Dinobothrium septaria* (see Woodland, 1927), and Southwell (1925) describes uterine pores in *Uncibilocularis trygonis* and *Balanobothrium tenax*.

That preformed pores and slits do exist extensively in the

Phyllobothriidae is, I think, abundantly proved, and I am therefore disposed to regard the equally-undoubted cases of apparent dehiscence as probably being secondary in nature and associated with vestiges of what originally were true pores. It is certain that some of the slit-like openings described as dehiscence-splits are not dehiscence in the true sense of the word, but modified true pores. This is well seen in the cases of *Dinobothrium septaria* and *Anthobothrium cornucopia*, e. g., in which the uterus opens freely to the exterior by concrescence of its walls with the ventral parenchyma and subcuticula long before the eggs could possibly accumulate in the shallow uterine cavity, and, as a matter of fact, they never do accumulate, being liberated immediately after they are discharged from the uterine duct.

NOTE ON *AMPHILINA PARAGONOPORA* (CESTODARIA).

In 1923 (Quart. Jour. Micros. Science, vol. lxvii. pp. 47-84) I published a description of a new species of *Amphilina* from India. In the course of that description I emphasized two features: the muscular nature of the huge "head" gland, which, with its gland cells and ducts, extends throughout the greater part of the body substance, and the occurrence of an "irregular-form stage" in the life of the worm. Though it is now almost superfluous for me to admit my error in describing the huge "penetration" (see Miller, Illinois Biol. Monogr., vol. x. No. 3, 1926) or cephalic histolytic gland as a "boring" muscle apparatus, yet it is as well to do so. My excuse for this absurd mistake is that I was at the time of studying this worm a novice in Helminthology and stationed in central India, away from all literature and fellow-workers. Further, although my description of the gland is correct in all its broad features, yet my sections were thick, and in consequence I was wholly unable to detect the gland duct lumina and openings at the anterior extremity, which can easily be seen in thin sections. The presence of such an enormous gland is still a matter of surprise to me and, assuming that its function is histolytic, it constitutes as good evidence as any muscular boring apparatus of the urgent necessity for the worm to make its way to the exterior from the body-cavity of its host.

As regards the "irregular-form" stage in the life-history of the worm, my description of the for-the-most-part shapeless masses which so largely occur in the fish coelom together with the active parasite, is perfectly correct, but I now believe that these masses are stages in the dissolution of the parasites by the tissues of the host, and therefore have nothing to do with the direct life-cycle. Despite the presence of the enormous "penetration" gland, the worm in a very large percentage of cases is apparently unable to escape from the fish and, sooner or later,

whether mature or immature, it dies, becomes encysted by the host tissues and is gradually disintegrated. I possess all stages of this process of dissolution—from the free or encapsulated egg-filled large worm down to the microscopic vestiges which I described in my paper.

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Reference Letters for Figs. 1-59 (Pls. I.-V.).

CS, cirrus-sac; DV, dorsal excretory vessel; EE, egg-ejector (Schluckapparat) EXC, excretory vessel; FC, fertilization chamber; L, terminal lappets; LM, longitudinal muscles; MED, medulla; N, lateral nerve; O, OV, ovary; OD, oviduct; SHG, shell gland; UOP, UTOP, uterine opening; UT, uterus; UTD, uterine duct; UTS, uterine sac; VAG, vagina; VD, vas deferens; VV, ventral excretory vessel.

EXPLANATION OF THE PLATES.

PLATE I.

Figures 1-14. *Echeneibothrium maculatum*, sp. n.

Fig. 1 (×175): the entire worm with a contracted rostellum. Fig. 2 (×56): scolex with phyllides showing no signs of loculi. Figs. 3-6 (×56): different forms and aspects of phyllides. Fig. 7 (×39): scolex with enormously extended rostellum. Fig. 8 (×180): longitudinal section through extremity of rostellum, showing the retracted pad and retractor muscles. Fig. 9 (×180): pad at extremity of rostellum in longitudinal section. Fig. 10 (×87.5): dorsal aspect of the ducts in the neighbourhood of the ovary. The outline of the uterine sac is omitted, likewise the numerous coils of the vagina, which latter duct is represented as having been pulled to the left side. Fig. 11 (×39): a ripe detached proglottid (ducts near ovary simplified). Fig. 12 (×180): transverse section through a mature proglottid in the region of the ovary (only the longitudinal muscle layer is shown, the subcuticula not being represented). Fig. 13 (×180): transverse section through the anterior region of a young mature proglottid. Fig. 14 (×260): egg (in optical section) preserved in formalin.

PLATE II.

Figures 15-27. *Echeneibothrium variabile*.

Figs. 15, 16 (×39): scolices (flattened) showing the crenulated outline (insertions of retractor muscles) of the base of the protrusible rostellar pad, and the irregular outline of the surface of the pad. Fig. 17 (×39): unflattened scolex, showing

hinged bothridia. Figs. 18, 19 ($\times 39$): the multiloculate condition of the bothridia. Figs. 20-22 ($\times 39$): scolices of young individuals (that of fig. 22 is much flattened). Fig. 23 ($\times 56$): longitudinal section through scolex, with retracted rostellar pad. Fig. 24 ($\times 39$): mature (unflattened) terminal proglottid. Figs. 25-27 ($\times 87.5$): transverse sections through the anterior region (fig. 25), cirrus-sac region (fig. 26), and ovary region (fig. 27) of a young mature proglottid.

PLATE III.

Figures 28-38. *Echeneibothrium* ("Discobothrium") *fallax*.

Figs. 28, 29 ($\times 39$): scolices (slightly flattened) showing the smooth surface (compared with *E. variabile*) of the rostellar pad and its spherical outline. Fig. 30 ($\times 39$): optical section across a bothridium, showing its sucker-like appearance. Fig. 31 ($\times 56$): bothridium with distinct loculi. Fig. 32 ($\times 17.5$): the *Tylocephalum*-like scolex (flattened) of a young specimen. The upper surface of the rostellum bears small spines. Fig. 33 ($\times 56$): longitudinal section through a scolex (for comparison with fig. 28). Fig. 34 (nat. size): whole specimen of *E. ("Discobothrium") fallax* (to the left) and of *E. variabile* (to the right), to show the characteristic differences of external form. Fig. 35 ($\times 27.5$): mature proglottid in surface view. Figs. 36-38 ($\times 56$): transverse sections through the anterior region (fig. 36), cirrus-sac region (fig. 37), and ovary region (fig. 38) of a mature proglottid, for comparison with figs. 25-27.

PLATE IV.

Figures 39-42. *Echeneibothrium julievansium*, sp. n.

Fig. 39 ($\times 39$): the scolex. Figs. 40-42 ($\times 70$): transverse sections through an immature proglottid in the anterior region (fig. 40), cirrus-sac region (fig. 41), and ovary region (fig. 42).

Figures 43, 44. *Scyphophyllidium giganteum*, gen. et sp. nov.

Fig. 43 ($\times 27.5$): the scolex. Fig. 44 ($\times 27.5$): the same in longitudinal section.

Figures 45, 46. *Anthobothrium cornucopia*.

Fig. 45 ($\times 39$): transverse section through a mature proglottid in the region of the ovary. Fig. 46 ($\times 39$): transverse section through the anterior region of a ripe proglottid to show the "*Solenotania*" type of uterus and its aperture.

Figures 47-49. *Phyllobothrium unilaterale*.

Fig. 47 ($\times 39$): the scolex. Fig. 48 ($\times 27.5$): transverse section through the anterior region of a ripe proglottid to show the large uterus and its small aperture. Fig. 49 ($\times 260$): the fibrillated sheet (in transverse section) separating the "medulla" from the "cortex."

PLATE V.

Figures 50-53. *Orymatobothrium musteli*.

Figs. 50, 51 ($\times 17.5$): scolices. Fig. 52 ($\times 56$): transverse section across mature proglottid in region of ovary. The absence of any line of separation of the "medulla" from the "cortex" contrasts with the distinct separation in *Phyllobothrium unilaterale*. Fig. 53 ($\times 12$): free detached proglottid, in ventral view, showing an early stage of development of the slit-like uterine aperture.

Figures 54, 55. *Calliobothrium verticillatum*.

Fig. 54 ($\times 12$): free detached proglottid, in ventral view, showing seven uterine pores (compare fig. 53). Fig. 55 ($\times 17.5$): another free proglottid showing the uterine sac and uterine pores in side view.

Figures 56, 57. *Acanthobothrium dujardini*.

Figs. 56 ($\times 87.5$), 57 ($\times 180$): transverse sections through the anterior region and ovary region respectively of a mature proglottid. Note the quadripartite ovary.

Figures 58, 59. *Onchobothrium pseudo-uncinatum*.

Figs. 58, 59 ($\times 39$): transverse sections through a young and old proglottid respectively to show the form of the ovary and general disposition of the organs. The "medulla" is distinctly separated from the "cortex."

35. New Species of Neuroptera Planipennia in British Collections. By P. ESBEN-PETERSEN, Silkeborg *.

[Received April 23, 1927: Read June 7, 1927.]

(Text-figures 1, 2.)

By the kindness of Mr. F. F. Laidlaw I have had the pleasure of studying three specimens of Ascalaphidæ, viz. *Balanopteryx locuples* Karsch from Lac Alaotra, Madagascar, an undescribed species representing a new genus from the same locality, and a new species of the genus *Protidricerus* v. d. Weele from the Philippine Isles, all in his collection.

LIDLAWIELLA, gen. n.

Tribe *Holophthalmineæ*.—Antennæ of the male strongly clubbed; reaching the pterostigma of the fore wing. Fore and hind wing unequally shaped; middle third part of the hind wing with a large and rounded dilation posteriorly. Both pairs of wings very narrow at base; the anterior ones with a long threadlike appendix near to the base posteriorly. Apical third part of the hind wing rather narrow. Abdomen of male slender and almost as long as the hind wing. Anal appendages of the male small and inconspicuous. Legs long and slender; tarsi as long as tibia; spurs almost straight, a little longer than the two basal tarsal joints together. Cu_{1a} and Cu_{1p} in the fore wing, and M_{2a} and M_{2p} in the hind wing form distinct right angles. Pterostigma short.

This new genus is nearly allied to *Balanopteryx* Karsch, but it is easily separated from that genus and from its other allies, viz. *Neomelambrotus*, *Protmesibasis*, and *Amæridops*, by its long antennæ, its peculiarly formed hind wings, and by the right angles between Cu_{1a} and Cu_{1p} in the fore wing, and between M_{2a} and M_{2p} in the hind wing.

Genotype is the species described below.

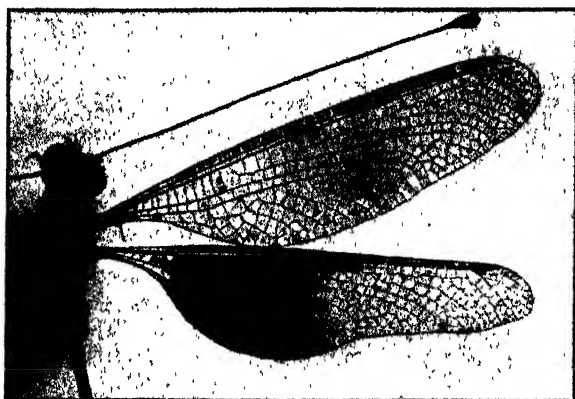
LIDLAWIELLA PULCHRA, sp. n. (Text-fig. 1.)

Antennæ reddish-brown; the club dark brown. Disc of thorax dark with small yellowish spots at the side margins and posteriorly; underside of thorax pale brown and with yellowish markings. Legs pale; fore and intermediate femora, and the outer margin of the tibiae brown; spurs, tarsi, and claws dark brown; hind tibiae with an indistinct brown ring at their apex, and a very narrow brown ring near their base. Abdomen blackish-brown above, pale below. Wings hyaline; costal area in both pairs of wings yellowish tinged; the basis

* Communicated by F. F. LAIDLAW, F.Z.S.

of the wings brown; in the basal half part of the hind wing a broad yellowish-brown transverse band with irregular lateral margins. Pterostigma dark brown. Apical areas of both pairs of wings rather broad and filled up by irregular rows of cells.

Text-figure 1.



Laidlawiella pulchra, gen. et sp. n.

Antennæ 29.5 mm.; fore wing 33 mm.; hind wing 32 mm.; abdomen of ♂ 28 mm.

1 ♂, holotype, Lac Alaotra, Madagascar.—To be deposited in the British Museum.

The body of the specimen rather dirty, and the description of the colour of the body and of its pilosity therefore rather insufficient.

PROTIDRICERUS PHILIPPINENSIS, sp. n. (Text-fig. 2.)

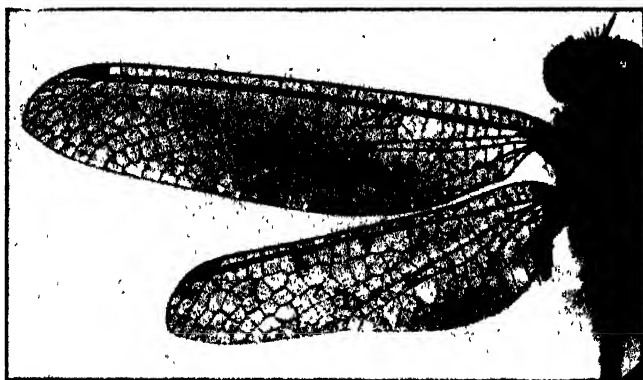
Antennæ jet-black. Head black; labrum and clypeus brown. Thorax black. Pilosity of head and thorax black. Legs brownish-black; tarsi, spurs, and claws dark brown. Abdomen very short, blackish, and with dark pilosity; posterior margin of abdominal segments narrowly brownish. Fore wings of equal breadth throughout; basal half part of hind wings broadened posteriorly; basal fourth part of costal area in the hind wing also broadened. Membrane of wings hyaline; pterostigma brownish-black; venation black. Five branches from R_s in both pairs of wings. The area between Cu_{1a} and posterior margin of the fore wing with three regular rows of cells (there is trace of a fourth row in the specimen at hand); the area between M_{2a} and posterior margin of the hind wing with only two rows of cells (this area is very short). Apical areas narrow, and each area with two rows of cells.

Antennæ 20 mm.; fore wing 28 mm.; hind wing 22.5 mm.; abdomen 15 mm.

1 ♀, holotype, Kolambugang, Philippine Isles.—To be deposited in the British Museum.

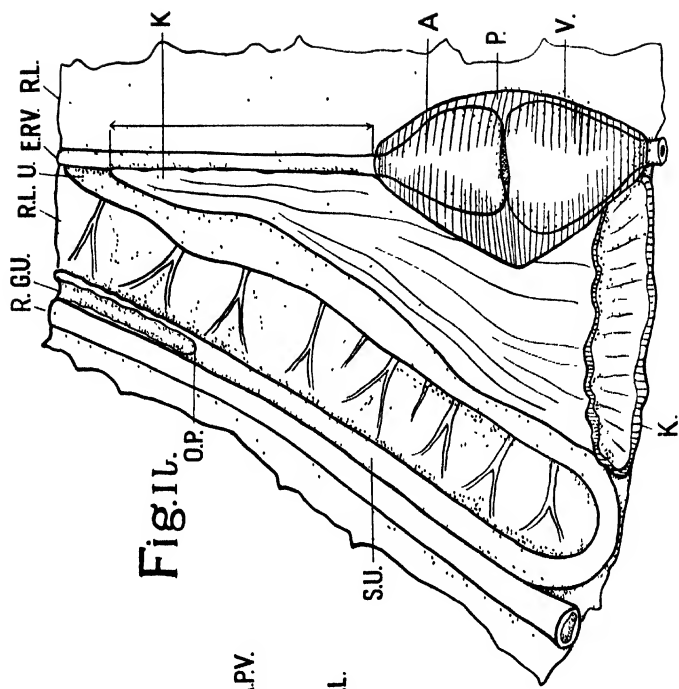
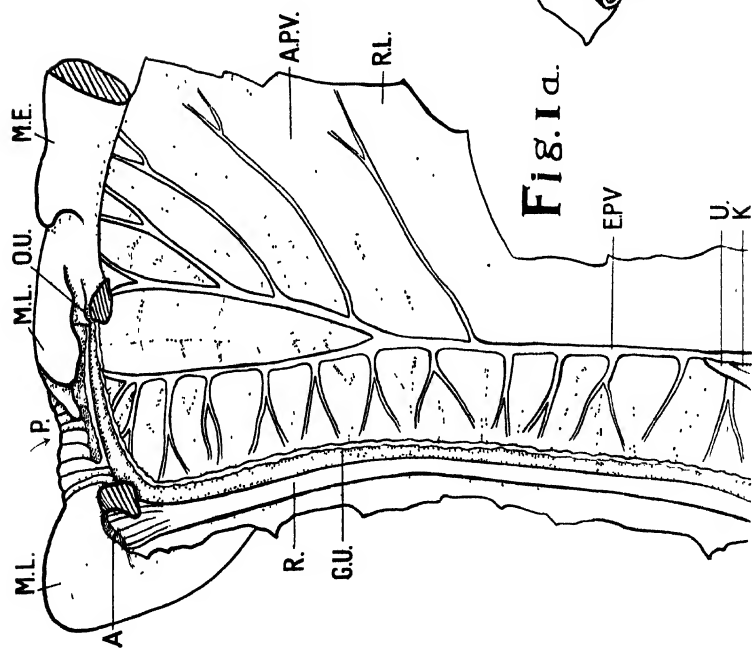
Four species of this genus are known: *exilis* MacLachlan from West China, *elwesi* MacLachlan from Assam, *japonicus* MacLachlan from Japan, and *irene* v. d. Weele from Borneo.

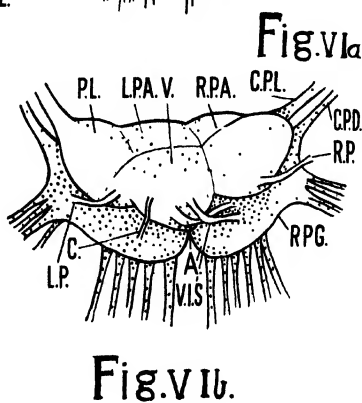
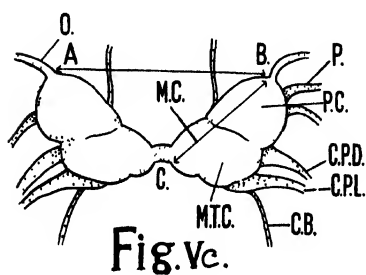
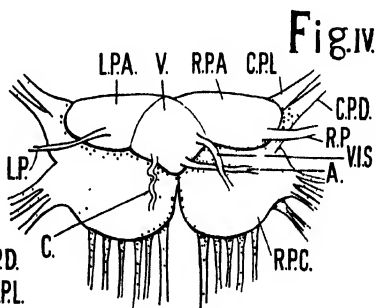
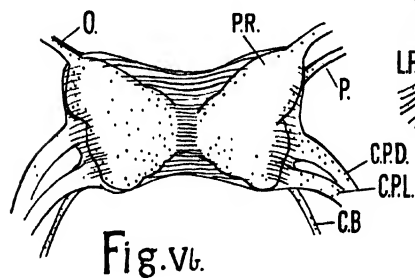
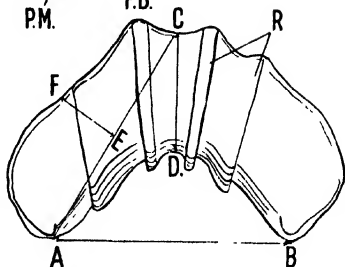
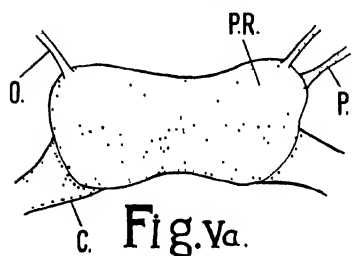
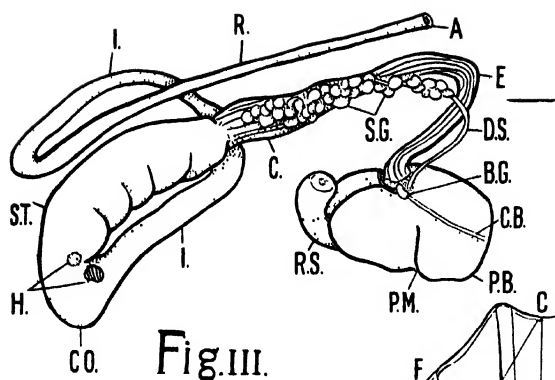
Text-figure 2



Protidricerus philippinensis, -p. n.

The new species is nearest allied to *elwesi* as to the shape of the wings; but it is easily separated from that species by its longer pterostigma, its narrower apical area, and by the more simple venation of posterior area. At first sight *P. philippinensis* has much likeness to *Nicerus gervaisi* Navas from China; but in that species the spurs are shorter than first tarsal joint, and the hind wings are narrower.





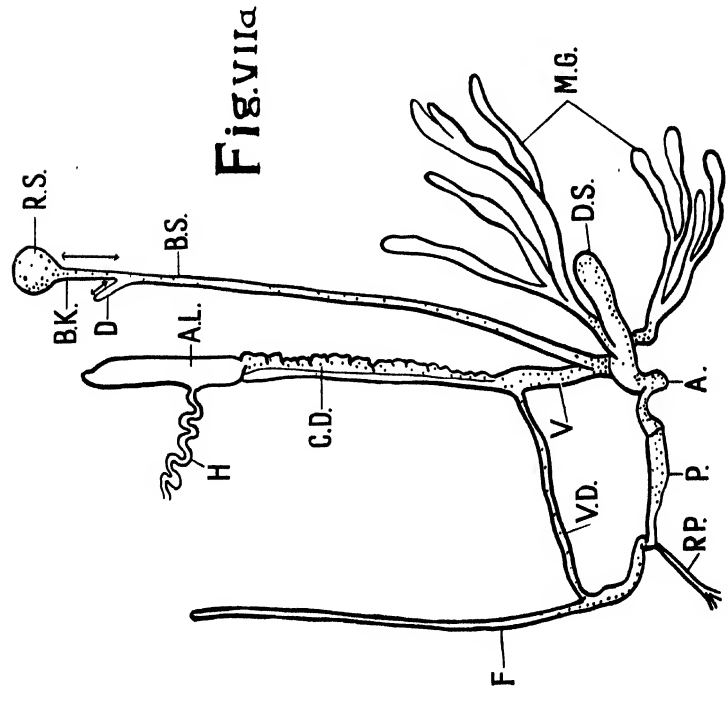


Fig.VIIa

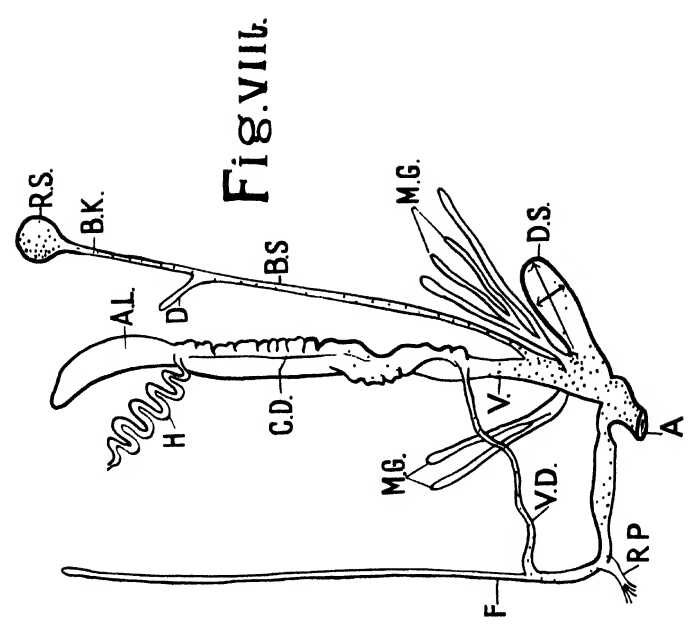
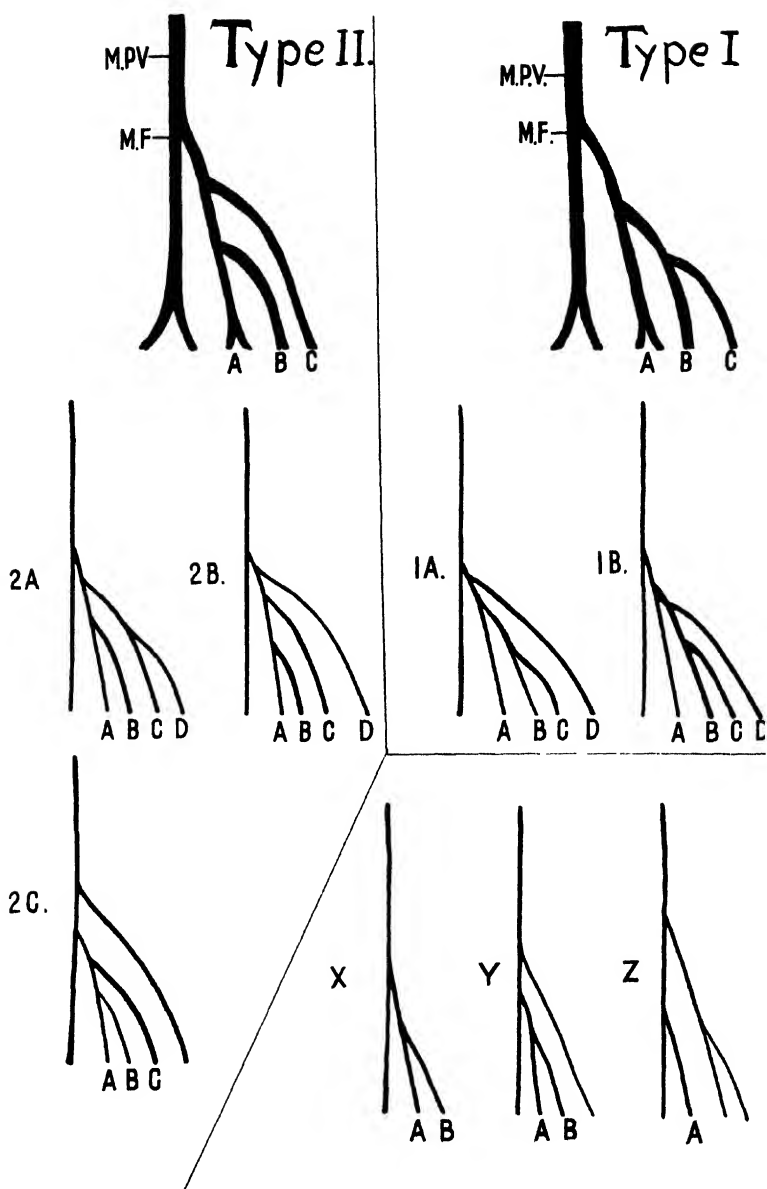


Fig.VIII.



ANATOMY OF *C. p. h.* and *C. nemoralis*.

36. On the Anatomy of the Land Snails (*Helicidæ*) *Cepæa hortensis* Müller and *Cepæa nemoralis* L. By DAPHNE AUBERTIN*.

[Received May 8, 1927 : Read May 24, 1927.]

(Plates I.-IV.†)

(Thesis approved by the University of London for the degree of M.Sc.)

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My best thanks are due to Mr. G. C. Robson for constant advice and assistance in the method of working at the problem, and in the presentation of the results. I must also thank Dr. E. M. Elderton for her advice on certain points.

The work was greatly facilitated by permission to use the Library of the British Museum (Natural History).

* Communicated by Dr. PHILIPPA C. ESDAILE, F.Z.S.

† For explanation of the Plates, see p. 581.

INTRODUCTION.

The land snails, *Cepæa hortensis* Müller and *Cepæa nemoralis* L., are recognized as distinct species by systematists on the strength of certain characters of the shell and genitalia (see pp. 555 and 556). It is uncertain, however, to what extent the rest of the structure of the two forms exhibits divergences which may be correlated with these differences.

The object of this paper is to furnish information concerning the amount of divergence between individuals of the two species as it is shown in organs not usually employed for the discrimination of closely-allied forms in this group of Mollusca. As a matter of convenience it is usually the practice, in the systematic treatment of the Pulmonata, to base the distinction between species on a limited number of characters selected from a certain part of the animal, *e. g.* the shell or the genitalia. It is of some interest, however, to ascertain to what extent divergence is shown in a number of different organ systems of two closely-related forms.

A statistical study of the amount of variability in a large number of characters of a species has been attempted previously, notably by Weldon (29) in the case of *Carcinus mænas*, and was extended by him to an analysis of the variability in different geographical races of *Crangon vulgaris* and *Carcinus mænas*, but all the characters dealt with in these studies were exoskeletal, and no attempt was made to study the internal parts statistically.

The present paper does not contain a description of every organ and part of individuals representative of the two species in question, but an attempt has been made to carry an analysis of their similarity or dissimilarity further than any previous work which has been undertaken on them, and to provide data on the variation of organs which have not as yet been dealt with by the taxonomist.

INTER-COLONIAL AND INTER-SPECIFIC DIFFERENCES.

The data presented here relate to (a) the differences between individual "colonies" of each species, it being now known that both of these snails tend to live in localized groups (colonies), and (b) the difference between the two distinguishable sets of individuals assigned to the species *Cepæa hortensis* and *Cepæa nemoralis*.

The morphological descriptions of organs are based on the whole of the material studied in each species. Inter-colonial differences only become apparent when the measurements relating to these organs are treated statistically.

If the data, produced by measuring a certain structure in the two conchologically divergent groups, are found to indicate some degree of overlap between the latter, it is of considerable interest to discover how this overlap is produced. Is it due to the sporadic occurrence of intermediate individuals, or is it incident to whole colonies? Not only is it interesting to ascertain this from

the general evolutionary point of view, but it is necessary also in systematic treatment to ascertain how far individual sections of a population are fair samples of the whole.

Since the two snails under consideration live in isolated colonies, it is possible that each colony may have a different constitution from that of other colonies, so that it becomes imperative to know exactly how far a sample taken from one such colonial assemblage differs from a sample from another colony. It is conceivable that differences justifying the recognition of two species might appear well marked when the material representing each group is drawn from a single colony of each species, but that these differences might become less exaggerated when further colonies of each form are studied.

Very little work of this type has been done on the Helicidæ. Klöti-Hauser (12) examined the genital organs, jaw, and radula of seven species of *Trichia*, measuring various parts with a view to establishing definite criteria for specific differentiation between them. He bases his conclusions on the measurement of about twenty specimens of each form, giving the range of variation and mean value for the measurements of the three organs under examination. He does not analyse his figures further by determining the Standard Deviation or Probable Error, and in most cases applies no correction for variation in size; it is therefore difficult to estimate the value of his results. He concludes, however, that it is possible to differentiate between the species in question by a careful comparison of measurements. The work of Lang (14) and Kleiner (11) will be dealt with later.

No anatomical work appears to have been published on inter-colonial variation.

CLASSIFICATION.

The two forms under examination are now placed in the subgenus *Cepæa* (Held, 1837) of the genus *Helix*, this having been generally accepted since about 1920. For a brief period they were kept in *Tachæa* (Leach, 1819) (*cf.* Pilsbry (21)), and are mentioned under this name by Bollinger (4) in 1909, who follows Kobelt's classification. This generic name was, however, preoccupied. Further synonyms will be found in the 'Synonymy of the British Non-marine Mollusca,' by A. S. Kennard and B. B. Woodward (10).

The earliest diagnoses of the species were based entirely on the shell, that of *C. hortensis* being differentiated from the shell of *C. nemoralis* by its smaller size, greater globosity, the colour of the lip, mouth index, and the angle made by the mouth in relation to the vertical axis. Lang (14) undertook a large number of measurements on the shell, and showed by this method, and by reference to the earlier work, that the shell characters intergraded to a certain extent, and did not therefore provide an absolute criterion of the species.

A. Schmidt (24) and Ashford (1) emphasized the importance of the dart in the classification of the Helicidæ. They describe the dart of both *C. hortensis* and *C. nemoralis*, and point out that it is impossible to mistake the one for the other. The dart in *C. nemoralis* is straight, with a definite neck between the head and the base, and the edges of the wings are entire, while in *C. hortensis* the dart is curved, there is no neck, and the wings are split.

Lang (14) and Kleiner (11) have stated that in the genitalia the flagellum is characteristic for each species, the relative length of flagellum to penis being longer in *C. nemoralis* than in *C. hortensis*; this character, however, overlaps in the two forms. They also found that the measurements and other characters of the dart and dart-sac show well-marked and discontinuous differences between the two forms, the length in *C. nemoralis* being greater than in *C. hortensis*, no overlap occurring in these measurements. They also noted specific differences in the mucous glands. Kleiner (11) has shown that the ratio of the upper part of the duct of the receptaculum seminis to the lower is characteristic for each form.

Bowell (5) has drawn distinctions between the radulæ of the two forms, based on measurements of the teeth and their basal plates.

Other differences between the two forms have been noted, but they have not been used taxonomically.

MATERIAL.

The material used consisted of about 200 examples of each species, collected from widely-separated localities.

The *Cepæa hortensis* were taken from six different colonies.

1. Suffolk Colony. Situated on a bank among bushes, brambles, and coarse grass. 44 specimens.

2. Iver Colony, Bucks. On a low bank beside a road, among coarse grass, dead nettle, convolvulus, ground ivy, and garden refuse. 56 specimens.

3. Knapp Hedge Colony, Wilts. On the top of a steep bank, among dogwood, brambles, and convolvulus. 30 specimens.

4. Chalke Bank Colony, Wilts. On a low bank by a road, among nettles, convolvulus, coarse grass, umbelliferous plants, and decaying vegetation. 30 specimens.

5. Meadow Hedge Colony, Wilts. On a low bank with a thick thorn-hedge, a road on one side and a water-meadow on the other, among nettles, ivy, and coarse grass. 30 specimens.

6. Hedge Lane Colony, Wilts. On a low bank, giving way to down, in coarse grass, shrubs, and umbelliferous plants. 30 specimens.

The Suffolk material was selected for certain shell-characters, namely pink ground-colour, brown lip, and absence of bands. These three characters are said to be genetically linked (Stelfox and Diver [MS.]).

The Wiltshire Colonies were all within a mile of one another but there was no possibility of the different populations becoming mixed.

The *Cepæa nemoralis* were taken from five different colonies.

1. Suffolk Colony. The animals were living completely associated with *C. hortensis* in the colony already described. 56 specimens.

2. Wembley Colony. On flat ground, surrounded by a bank, among coarse grass, chickweed, nettles, ragwort, and a few umbelliferous plants. 50 specimens.

3. Nanjizal Colony, Cornwall. Beside a stream among granite rocks, coarse grass, nettles, and brambles. 40 specimens.

4. Maiden Castle Colony, Dorset. Among coarse grass on a down. 40 specimens.

5. Seaton Colony, Devonshire. On a bank with a low thorn-hedge at the top, beside a road, among thyme, coarse grass, briar, gorse, and nettles. 40 specimens.

The material was collected during the years 1921 to 1926.

The specimens from Iver were fixed in Bouin's fluid and then transferred to alcohol. The Nanjizal material was drowned and then placed in alcohol. The rest of the material was killed by short immersion in boiling water, and was then preserved in 95 per cent. alcohol. It was all in good condition.

Each body was numbered when removed from its shell, and a corresponding number attached to the shell.

METHOD.

The data presented in this paper relate to the heart, pulmonary veins, kidney, ureter, nervous system, and genital organs, and consist of measurements and summary descriptions of parts not susceptible to measurement.

The measurements were tabulated under the number of the animal from which they were taken, and were recorded as a percentage of the height of the shell. The material was examined in the following way.

The external pigmentation and general appearance of each animal was noted. The roof of the lung was then removed with the heart, kidney, rectum, and ureter. These organs were examined and measured from the inner surface, under water. All dissection was carried out under a binocular dissecting microscope, as were also the measurements, which were made with

a pair of screw dividers and a steel ruler, graduated to 0.5 of a millimetre.

After examination of the lung and adjacent organs, the genital organs were removed and preserved for examination. The oesophagus was then cut just behind the buccal bulb, and the alimentary canal and liver removed.

The cerebral ganglia were examined and measured. After removal of the jaw and radula for further examination, the buccal bulb was turned forwards on separating the retractor-pharynx muscle from the columellar muscle, and the sub-oesophageal nerve mass was examined.

The insertions of the retractor muscles of the foot and the retractor pharynx muscle were noted, but yielded no results of any interest.

All the measurements taken were such as could be determined with accuracy to 0.5 mm.

In obtaining data, particularly of a quantitative kind, it is important to evaluate the effects of (1) age, (2) sex, and (3) environment.

(1) Age in *C. hortensis* and *C. nemoralis* is easy to estimate within certain limits. The young forms become mature within a year, and on reaching maturity the growing edge of the shell becomes thickened and forms a "lip," which indicates that the growth of the shell has ceased. At approximately the same time the animal becomes sexually mature. The distinction between mature and immature genital organs is easily recognizable, and, taken in conjunction with the condition of the free edge of the shell, it is possible to reject all forms which have not attained to their full size or are not sexually mature. Ideally the animals used should be of identical age, and one would have to decide whether they should be classed in years, half-years, or months; but the animals probably do not live for more than three years*, and, as the lip is formed at the end of the first year, it would be hardly worth while to consider changes which might occur during the second and third years.

A number of young forms with partially-thickened lip and immature genital organs were examined. As a result, significant differences in variability of the organs in young and old forms were found which might be due to difference in age (Table 1.). To avoid a possible error, immature forms were excluded from the material.

Only twelve young *C. hortensis* were examined as against twenty-six *C. nemoralis*. The results are tabulated below, but the numbers in the case of the former species are extremely small to form the basis of the calculations.

* Some of Lang's (14) snails lived for as long as six years in captivity. Hazay (9) gives three years as the greatest age attained by *C. hortensis* and *C. vindobonensis*, living freely.

TABLE I.

Organ.	<i>Cepæa hortensis</i> .					<i>Cepæa memoralis</i> .				
	Adult. M.	Young. M.	Diff.	P.E.D.	Sig.	Adult. M.	Young. M.	Diff.	P.E.D.	Sig.
Ventricle ...	14.9	12.6	2.3	.4	Sig.	14.5	11.8	2.7	.1	Sig.
Auricle	13.2	10.5	2.7	.4	"	13.5	10.6	2.9	.2	"
Pericardium .	16.9	14.3	2.6	.3	"	18.9	14.9	4.0	.3	"
Kidney	34.9	29.2	5.7	.7	"	40.9	36.4	4.5	.9	"
M.P.V.	77.5	72.5	5.0	1.7	—	87.1	75.4	11.7	1.8	"
F.U.	154.4	52.5	1.9	1.5	—	55.3	49.7	5.6	1.6	"
L.O.N.	15.9	15.1	.8	.4	—	14.7	13.9	.8	.3	—
L.C.G.	8.9	8.6	.3	.3	—	7.8	7.1	.7	.1	Sig.

M. Mean.

Diff. Difference between means.

P.E.D. Probable error of difference between means.

Sig. Significance of difference.

M.P.V. Main pulmonary vein.

F.U. Distance from fork to ureter.

L.O.N. Distance between roots of optic nerves.

L.C.G. Length of cerebral ganglion.

The nature of the measurements to which these figures refer will be found for the Ventricle..... .. page 566

Auricle " 566

Pericardium " 566

Kidney " 565

Pulmonary vein..... .. " 565

Fork to ureter " 565

Distance between optic nerves. .. " 570

Cerebral ganglion " 570

(2) Sex is obviously of no account in the present case, since the animals are hermaphrodite.

(3) The ecological character of the habitats from which the material has been drawn has already been described.

The present paper deals with actual phenotypic differences between the two species, and it is not part of its aim to distinguish between hereditary and environmental differences. The data obtained refer to variation which may be due to both hereditary and environmental differences, my object being to detail its occurrence rather than to assign to it any particular significance.

ARRANGEMENT OF RESULTS.

The method followed for the statistical presentation of the results has been the determination of the Mean value, Standard deviation, and Probable error for each organ. In this way an

indication of the relative variability of any organ in the two forms can be compared. It is also possible to compare the variability of all the organs in one form.

Where the mean value for any organ is very close in the two species, the significance of the difference between the two means has been tested by the method proposed by Rietz and Smith (2), e.g. a difference is considered significant if it is three times as large as its probable error.

STRUCTURE.

External Features.

C. hortensis and *C. nemoralis* are typically banded snails in which the ground-colour of the shell is frequently yellow, but variation in both banding and ground-colour occurs. *C. hortensis* is, on the whole, somewhat smaller than *C. nemoralis*, but they overlap in size, so that this distinction is not absolute. The bodies are generally pigmented, and have a longitudinal unpigmented stripe running from the head to the anterior border of the lung.

The pigmentation of the foot-sole may be different in the two forms. In *C. nemoralis* the pigment is concentrated in a band which follows the outline of the foot-sole round the posterior end, leaving a light margin. The most heavily pigmented portion lies posteriorly. In *C. hortensis* the anterior part of the foot-sole is pigmented and the posterior end devoid of pigment. This fact is noted by Binney (3); he states that the base, by which he probably means the anterior part of the foot, is inky, while the posterior part is a dirty flesh-colour. Lehmann (17) refers to the foot-sole in *C. hortensis* as whitish. A general account of the external appearance and pigmentation is given by Lehmann (17) and by Moquin-Tandon (19), but no features of diagnostic value emerge from these descriptions. The contrast in the foot-soles is not an absolute means of distinction, since albinos occur in both forms and the intensity of pigmentation varies. Some of the *C. hortensis* from the Chalke Bank Colony were characterized by very heavy pigmentation on the body.

The pneumostome lies on the right side of the animal, and is stated by Moquin-Tandon (19) to be about 2 mm. broad in *C. nemoralis*. Binney (3) notes that in *C. hortensis* it is surrounded by a ring of pigment, but this was not observed in any of the specimens examined.

The ureter opens to the exterior to the left of the pneumostome, and the anus to the right of it. Both these openings are guarded by small grooved projections of the body-wall. The grooves lead away from the pneumostome, and may possibly serve to keep it free of the excreta. Moquin-Tandon (19) states that in *C. nemoralis* the "Lobe fécal" is triangular, and that in *C. hortensis* it is not outstanding. The shape of these lobes is not very characteristic in either form, and cannot be used to distinguish them from one another.

Shells.

A vast amount has been written concerning the shells of *C. hortensis* and *C. nemoralis*, dealing mainly with the variation in banding and ground-colour. These variations have been regarded by some as adaptive, and possessed of selective value, but no body of evidence exists to bear out these views. Schilder (22) in a recent paper concludes that banding and ground-colour are independent of one another. The inheritance of banding and certain ground-colours has been demonstrated beyond doubt by Lang's genetical work on *C. hortensis* and *C. nemoralis* (14 & 15). More recent work by Stelfox (26) is in accordance with this.

Schilder (23) and others have evidence that type of banding and ground-colour may be regarded as colonial characteristics, and that they vary in frequency from one colony to another. Table II. bears this out.

Coutagne (6) states that if the two species occur in the same locality, it is generally easy to separate the one from the other by inspection of their shells; if, however, *C. hortensis* and *C. nemoralis* from different localities are compared, it is often very difficult or impossible to "place" a certain number of the specimens.

The present study is concerned with the soft parts rather than with the shell. As no correlation was found between the type of shell and other characters, *e. g.* the flagellum, within each species, the shell-characters are dealt with very briefly in the following table, for the use of which I am greatly indebted to Captain Diver.

TABLE II.

Ground-colour.	<i>Cepæa hortensis.</i>					<i>Cepæa nemoralis.</i>				
	K.	C.	M.	H.	I.	N.	W.	S.	M.C.	Seaton.
	%	%	%	%	%	%	%	%	%	%
Brown ...	21·8	30·0	56·6	3·3	—	—	—	3·8	15·0	7·7
Pink	9·3	6·6	3·3	—	8·4	43·5	52·7	40·4	77·5	56·4
Yellow ...	68·7	63·3	36·6	90·0	87·4	56·4	46·4	55·7	7·5	35·9
White	—	—	3·3	6·6	1·4	—	—	—	—	—
Banding (most frequent).										
12345	37·5	53·3	63·3	39·9	74·6	15·3	44·4	65·4	65·0	71·8
00800	—	—	—	—	—	41·0	35·6	8·2	27·5	7·7
00000	62·5	46·6	36·6	60·0	24·0	43·6	18·7	14·3	7·5	20·5

K. Knapp Hedge.
C. Chalke Bank.
M. Meadow Hedge.
H. Hedge Lane.
I. Iver.

N. Nanjizal.
W. Wembley.
S. Suffolk.
M.C. Maiden Castle.

The mean value, and range of variation of the height of the shell were determined for each form.

In the following table the frequency lists for the shell-height in each colony are given. The table shows that in each colony the shell-height varies around its own particular mean in the normal fashion.

TABLE III a.

Cepaea hortensis.

Shell-height (mm.).	Knapp Hedge.	Chalke Bank.	Meadow Hedge.	Hedge Lane.	Suffolk.	Iver.
11	8	1	1	5	1	3
11.5	5	3	—	2	2	1
12	11	3	7	11	11	9
12.5	4	—	4	4	6	5
13	1	14	16	6	7	21
13.5	1	8	1	2	3	2
14	—	1	—	—	4	7
14.5	—	—	1	—	—	—
15	—	—	—	—	—	2
Mean value (mm.).	11.9	13.0	12.9	12.3	12.8	13.0

TABLE III b.

Cepaea nemoralis.

Shell-height (mm.).	Nanjizal.	Maiden Castle.	Seaton.	Wembley.	Suffolk.
11.5	—	1	—	—	—
12	—	2	—	1	—
12.5	—	6	1	—	2
13	—	15	4	1	8
13.5	1	5	2	4	4
14	5	9	17	25	9
14.5	3	1	3	3	2
15	15	1	10	5	5
15.5	7	—	1	3	—
16	6	—	1	1	—
16.5	1	—	—	—	—
17	2	—	—	—	—
Mean value (mm.).	15.4	13.4	14.4	14.4	14.0

Bands and Pigment on the Roof of the Lung.

The observations were made on about 100 individuals of each form.

The roof of the lung cavity in both forms varies greatly in accordance with the presence or absence of pigment, and of longitudinal reddish bands in the anterior part.

The pigment, when present, is bluish-grey or black, and may be scattered thickly or thinly all over the roof of the lung. It occasionally encroaches on the lower surface of the pericardium and kidney. When the roof of the lung is heavily pigmented, the pulmonary vessels are rendered conspicuous by the absence of pigment from them, and its concentration alongside of them. This appearance would make one think that the vessels form a barrier to the free migration of pigment through the subcutaneous tissue.

Of the Suffolk *C. hortensis* fourteen were entirely devoid of pigment, thirteen had a light patch of pigment over the pneumostome, and the remaining fifteen had pigment all over the roof of the lung. In those from Iver, none of the animals had any pigment on the lung, except, in one or two cases, a faint patch over the pneumostome. In the *C. nemoralis* from Suffolk, about half the number of forms examined were pigmented, while in those from Wembley the majority showed pigmentation.

In a large number of the forms examined, longitudinal reddish stripes were found on the anterior part of the roof of the lung, varying in number from one to five.

Lehmann (17), in his description of *C. nemoralis*, notes that the bands on the mantle accord with the bands on the shell. This coincidence of bands has formed the subject of a paper by Distaso (8), who considered the matter important in connection with Lang's work (14) on the inheritance of shell-bands in *C. hortensis*, *C. nemoralis*, and their hybrids.

Distaso examined large numbers of the two species in question, and found in all cases a strict agreement between the bands on the mantle and the bands on the shell of each individual. The bands on the mantle were reduced in length, and were indicated posteriorly by flecks as the pigment became less concentrated. The bands ran forward on the lung and terminated just before the junction of the lung and body-wall, at the mantle-groove. He noted that in *C. nemoralis*, with a pigmented lip to the shell, this groove was pigmented, while in *C. hortensis*, with a white lip to the shell, the groove was unpigmented and less noticeable. Distaso went on to state that in forms where the shell-bands were fused the bands on the mantle were also fused, and that, if bands were missing on the shell, they were also missing on the mantle. He then deals histologically with the formation of the bands on the mantle and their repetition in the shell. He regards the shell-bands as dependent on mantle-bands, and the mantle-bands on the presence or absence of pigment-forming cells in the subcutaneous tissue. He concludes, therefore,

that variation in shell-banding is the outcome of a histological variation connected with the pigment-cells, and that in the light of Lang's work this histological variation is inheritable. Distaso implies that he found complete coincidence between the bands on the mantle and the bands on the shell.

In the animals examined for the purpose of work, complete coincidence was not found in a large number of cases, although it was obvious that some connection existed between two sets of bands.

In the Suffolk *C. hortensis* the shells were all unbanded, and no bands were found on the roof of the lung. In the *C. nemoralis* from Suffolk 38 per cent. agreed perfectly, 19 per cent. agreed in the number of bands, but the bands on the mantle were either not fused or were less fused than those on the shell; 25 per cent. had fewer bands on the mantle than on the shell; the reverse was the case in 10 per cent., and in 6 per cent. the shells had an abnormal band which found no counterpart on the mantle.

In the *C. nemoralis* from Wembley, 62 per cent. were in perfect agreement, 25 per cent. agreed in the number of bands but not in the degree of fusion, and 11 per cent. had fewer bands on the mantle than on the shell. In the last class the bands which were absent from the mantle were in all cases except one found to be weakly represented on the shell. In another member of this class the bands on the shell were hyaline*, the formula being 123(45); the mantle had no trace of bands.

The *C. hortensis* from Iver showed considerably less agreement than the Wembley *C. nemoralis*. 42 per cent. were in perfect agreement; in 9 per cent. the number of bands were the same, but no fusion occurred in the mantle-bands, while the bands on the shells were fused in varying degrees. In 14 per cent., where all the shells were of the formula 12345, the mantle had fewer bands; while in 33 per cent., where the shell-band formula was again 12345 and the bands exhibited every degree of fusion, bands on the mantle were entirely absent.

These observations are difficult to reconcile with Distaso's conclusions that the bands on the mantle and the bands on the shell are due to the same cause and are dependent on one another.

Afferent and Efferent Pulmonary Vessels.

The roof of the lung is divided longitudinally into two parts by the efferent pulmonary vessel running back to the auricle (Pl. I. figs. 1 a & 1 b). Nalepa (20) noted that the character of the internal wall differed in the two halves. He states that the part on the right lying between the pulmonary vein and the rectum is raised up into ridges, in which the blood-vessels lie; he describes the part on the left as having a flat inner surface.

* i. e. the shell is modified in the position of the bands, but lacks the band-pigment.

This is true for the posterior two-thirds, but anteriorly, where the respiratory exchange takes place most actively, the internal surface is raised up into ridges as on the right side.

G. Schmidt (25) has studied the pulmonary circulation in *Helix pomatia*, and also contrasts the type of circulation in the right and left sides of the lung, noting that in the posterior two-thirds of the left side the vessels are small and very few, while on the right side there is a well-developed circulation reaching to the posterior end of the lung.

In the two species under discussion the venous blood is brought to the lungs by two veins, which unite to form a transverse vein in the anterior part of the lung. This vein gives off afferent branches, aeration taking place while the blood passes through the lacunæ lying in the subcutaneous tissue of the roof of the lung on its way to the efferent vessels. Variation occurs, as Schmidt (25) observed for *Helix pomatia*, in the branching of the efferent pulmonary vessel. The branching in *C. nemoralis* and *C. hortensis*, as for *Helix pomatia*, is of three orders; the variations and relative frequency of their occurrence will be dealt with later.

The following three measurements were taken :—

(a) From the anterior end of the pericardium to the apex of the kidney. (Length of kidney.)

(b) From the tip of the primary ureter to the main fork of the pulmonary vein. (Main pulmonary vein.)

(c) From the main fork of the pulmonary vein to the external opening of the ureter. (Fork to ureter.)

(Pl. I. figs. 1 a & 1 b.)

The figures obtained for each colony will be found on Tables IV. and V. The mean values vary considerably from colony to colony, but the standard deviation remains fairly constant in each species.

Diagrams of the main types of circulation in the lung are shown on Pl. IV.

The most generalized type of branching in the vessels is probably that shown in Type I. (Pl. IV.); this view is taken by Schmidt (25) for *Helix pomatia*, as this type shows the three orders of branching in their simplest form. The main stem of the pulmonary vein runs down the roof of the lung parallel to the rectum, and terminates at the anterior junction of the lung and body-wall. This main stem invariably gives off a branch, *a*, forming the main fork in the measurements previously dealt with. In the circulation figured in Type I. (Pl. IV.) the branch *a* gives off a branch of the second order, *b*, and *b* gives off one of the third order, *c*. Each of these branches forks at its termination, and may give off small lateral branches; the afferent pulmonary veins alternate very regularly with the branchings of the efferent veins.

Variation in the origin of the branches is common, and the type of branching described above is not that which is found most frequently in either of the two species under discussion.

The most usual type of branching found in *C. hortensis* and *C. nemoralis* is Type II. (Pl. IV.), where *c* is not given off from *b*, but originates from *a*.

The frequency of occurrence of the different types is given in the following table. About 100 bodies of each species were examined in this respect.

	Type I.	Type Ia.	Type Ib.	Type II.	Type IIa.	Type IIb.	Type IIc.	Type X.	Type Y.	Type Z.
	%	%	%	%	%	%	%	%	%	%
<i>Cepæa hortensis</i>	18.3	2.2	0	62.4	4.3	10.8	1.1	2.2	4.3	0.0
<i>Cepæa nemoralis</i>	17.4	0.0	1	53.0	1.0	7.0	6.1	2.0	8.2	1.2

From this table it will be seen that the majority of individuals in both forms follow Type II., while an appreciable number follow Type I. In accordance with this, there are fewer variations on Type I. than on Type II.

Schmidt (25), with reference to *Helix pomatia*, says that the afferent pulmonary vessels vary very little in branching. In *C. hortensis* and *C. nemoralis* the afferent veins invariably alternate with the efferent veins, and therefore any variation in branching of the efferent veins is accompanied by a corresponding variation in branching of the afferent veins.

Heart.

The heart (Pl. I. fig. 1 b) consists of a pear-shaped auricle and ventricle, enclosed in a fusiform pericardium. It lies to the left on the inner surface of the posterior end of the roof of the lung, closely opposed to the kidney, which is situated to the right of it. The main pulmonary vein enters the auricle anteriorly, and the aorta leaves the ventricle posteriorly. Lehmann (17) describes that of *C. nemoralis*, stating that the auricle is 2 mm. long, rather thinner in appearance than the ventricle and concave posteriorly, while the ventricle is 2.5 mm. long. He makes no mention of the heart in *C. hortensis*. Taylor (27) notes that in this species the heart has a large white ventricle and smaller brown auricle.

In the material examined the auricle was found, as a general rule, to be smaller than the ventricle, but as the heart is a contractile organ, this is of little significance. The measurements taken on the heart were: (a) the length of the ventricle; (b) the length of the auricle; (c) the greatest width of the pericardium (Pl. I. fig. 1 b). The figures obtained will be found in Tables IV. and V.

Ureter.

The morphological structure of the ureter in the Pulmonata has been dealt with by Lang (16), and several of the varying

conditions are figured by him; but he makes no mention of *C. hortensis* and *C. nemoralis* in this connection, and no description of the ureter appears to exist.

The primary ureter originates as a tube at the apex of the kidney (Pl. I. fig. 1 b). It turns sharply backwards and runs along the right side of the kidney closely opposed to it. At the posterior end of the kidney it merges in a U-shaped bend with the secondary ureter. The latter runs forward close to the rectum. After running about a third of its course the secondary ureter becomes an open groove; this groove continues alongside the rectum until it reaches the anterior junction of the lung and body-wall, where it takes a right-angled turn to the left and runs over the pneumostome, to the left of which it opens to the exterior between two small pallial lobes. (Pl. I. fig. 1 a.)

The position at which the secondary ureter becomes a groove is of importance in connection with distinctions between *C. hortensis* and *C. nemoralis*. There appears to be a tendency in *C. hortensis* for the ureter to open into a groove behind the apex of the kidney, and in *C. nemoralis* for it to open in front, although a certain amount of overlap occurs.

Alimentary Canal.

Apart from the jaw and radula, very little reference to the alimentary canal of *C. hortensis* and *C. nemoralis* is to be found. It agrees in general structure with that of *Helix pomatia*, described by Meisenheimer (18). The œsophagus, which leaves the pharyngeal bulb above the radular sac, is longitudinally striated. It passes through the nerve-ring and runs backwards, passing insensibly into the crop. This dilatation passes gradually into the stomach; this region lies between the lobes of the liver, under the albumen gland. (Pl. II. fig. 3.) Nalepa (20) has stated that the stomach is merely a swelling of the gut and shows no histological differentiation.

At the posterior end of the stomach there is a blind diverticulum receiving the openings of the two hepatic ducts. The intestine originates from the diverticulum, runs forward below the stomach, forms two coils in the left lobe of the liver (Pl. II. fig. 3), and passes into the rectum. The rectum runs forwards on the right of the lung, the anus opening to the right of the pneumostome close to a small pallial lobe.

The liver varies in colour from pale yellow to dark brown or slate-grey.

The salivary glands are paired white flocculent bodies which lie closely opposed to the anterior part of the alimentary canal; the salivary ducts run forward and open into the mouth close to the buccal ganglia and to the origin of the œsophagus, after passing through the nerve-ring and the muscles of the pharyngeal bulb.

In *C. nemoralis* the salivary glands lie on the crop, as in *Helix*

pomatia and others of the *Helicidae*, but Taylor (27) states that in *C. hortensis* they lie on the œsophagus. The glands, however, vary greatly in length and are uncertain in outline, and the distinction between the œsophagus and crop is not readily noticeable, so that this contrast between the two forms is probably of no great value.

After examination of the alimentary canal in 100 specimens of each species, no variation was found in the coiling of the intestine or in the branching of the hepatic ducts and the position of their openings. There were no features which could have been satisfactorily measured.

Jaw.

The jaw (Pl. II. fig. 4) in *C. hortensis* and *C. nemoralis* has been described frequently. Lang (14) gives the descriptions from Busch, Moquin-Tandon, Lindström, Kobelt, and Lehmann.

Kobelt (13) counted the ridges on the jaw in 100 of each species, and found that they varied from 2 to 7 in *C. hortensis* and 2 to 9 in *C. nemoralis*, and that they were seldom arranged symmetrically. He draws a distinction between main and subsidiary ridges, and finds that when all are taken into account, the mean number for the former is 3·7 per cent. and for the latter 4·6 per cent.

161 jaws of each species were examined. The number of ridges was found to vary from 2-6 in *C. hortensis* and 2-8 in *C. nemoralis*. The results agree fairly well with those of Kobelt, and are given in the table below. No marked colonial variation was noted.

No. of Ridges.	<i>Cepæa hortensis.</i>	<i>Cepæa nemoralis.</i>
2	16·1 per cent.	1·2 per cent.
3	33·5 "	4·9 "
4	30·4 "	32·3 "
5	15·5 "	34·1 "
6	4·3 "	22·3 "
7	—	4·3 "
8	—	0·6 "

Taylor (27) states that the ridges increase in number with age. This may be true for the first year while the snail is still immature, but a number of young forms examined had six ridges on their jaws. These forms had just begun to form a lip, and were therefore nearly sexually mature. Since they had as large a number of ridges as were found in the majority of mature forms, it is unlikely that they would continue to form ridges during their adult life.

The length AB and the width CD of the jaw (Pl. II. fig. 4) were measured on thirty-three *C. hortensis* and twenty-seven

C. nemoralis. No significant differences between the two species were found for either measurement, but the numbers used were rather small to base calculations on.

Radula.

Lang (14) has collected the descriptions of the radula of these two species written by Busch, Lehmann, and Pilsbry.

These writers lay stress upon the number of longitudinal and transverse rows of teeth, but they do not agree on this point. It is evident, however, that *C. hortensis* has fewer longitudinal and more transverse rows than *C. nemoralis*. The median tooth is supposed to be rather smaller than the lateral teeth in *C. nemoralis* and about the same size in *C. hortensis*.

Bowell (5) gives a detailed account of the radula based on measurements of selected typical specimens. He does not think that the number of longitudinal and transverse rows of teeth is of any value as a criterion for distinguishing the two species, since the teeth at one end are not fully formed, those at the other end are worn down, and the marginals are often reduced. He has taken measurements of the length and breadth of the basal plate, and measurements of the teeth for median, lateral, and marginal unci, and finds that specific differences can be detected in this way. He also contrasts the shape of the basal plates.

Bowell does not give the number of specimens on which he bases his numerical results, and further states that the specimens selected are typical. It is impossible to tell, therefore, if his results would hold for the examination of a large number of unselected specimens which might show a considerable amount of individual variation. In the present paper no measurements of the radula teeth are given, but differences were noted in their shape and the shape of the basal plates, these sufficing to show that the radula is different in certain respects in the two forms.

No inter-colonial observations were made on this structure.

Nervous System.

The central nervous system of *C. hortensis* and *C. nemoralis* does not appear to have been described in detail.

As in *Helix pomatia*, concentration of the ganglia has occurred. The cerebral ganglia lie above the œsophagus, and the sub-œsophageal nervous mass is composed of fused pleural, parietal, and visceral ganglia, and the closely-associated pedal ganglia.

The cerebral ganglia are enclosed in a thick coat of connective tissue. The thickness and pigmentation of this connective tissue vary considerably. It appears to be somewhat thicker in *C. nemoralis* than in *C. hortensis*, since in the former it is generally impossible to see the shape of the ganglia before it is removed, while in the latter the outline of the ganglia is always visible. In the one the connective tissue enclosing the

ganglia forms a transverse strap (Pl. II. fig. 5a) lying across the buccal bulb, while in the other it tends to conform more to the shape of the ganglia, although the strap-like appearance is occasionally met with (Pl. II. fig. 5b). The pigment characteristic of the majority of forms examined in both species (100 of each) is distributed uniformly in the connective tissue in *C. hortensis*, but in *C. nemoralis* it is conspicuously absent in the region of the protocerebrum of each cerebral ganglion. This absence of pigment makes the protocerebra stand out as two well-marked white, oval patches, which can be observed at once when examining the ganglia (Pl. II. fig. 5a).

This contrast in appearance of the cerebral ganglia is very typical of the two forms, but does not amount to an absolute distinction, since in a few cases *C. nemoralis* was found to resemble the "*hortensis*" type, and the converse also occurred. In the forms examined, 96 per cent. of the *C. nemoralis* and 94 per cent. of the *C. hortensis* were typical.

In a certain number of both species, pigment was entirely lacking over the cerebral ganglia. In a number of cases this was associated with immaturity in the reproductive organs, but this was not invariably so.

Variation was found to occur in the appearance of the cerebral commissure. In general it was found to be about 0.5 mm. long in either form, but specimens were found in both species, where it was either abnormally long or so short as to be invisible externally. The latter condition was found to occur in 8.4 per cent. of the *C. hortensis* and in 10.3 per cent. of the *C. nemoralis*. In 6.3 per cent. of the former and 8.7 per cent. of the latter the commissure was abnormally long. No correlation was found between sexual immaturity and the condition of a long cerebral commissure.

Two measurements were taken on the cerebral ganglia. The distance AB (Pl. II. fig. 5c) between the roots of the optic nerves was measured, and also the distance BC (Pl. II. fig. 5c) from the origin of the cerebral commissure to the root of the optic nerve on the same side. In both forms the absolute measurements were remarkably constant, the distance between the roots of the optic nerves being generally 2 mm. and the length of the ganglion 1 mm. The figures obtained will be found on Tables IV. and V.

The subesophageal nerve mass is also similar in composition to that of *Helix pomatia*, which has been described by Meisenheimer (18).

The paired pedal ganglia give off numerous nerves to the foot, while the mantle and viscera receive nerves from the visceral nerve mass. The cephalic aorta runs between this mass and the pedal ganglia.

The visceral nerve mass is composed of paired pleural and parietal ganglia and the unpaired visceral ganglion. The latter is completely fused with the left parietal ganglion as in *Helix*

pomatia. All the ganglia lie very closely together, and are only to be distinguished from one another by grooves on the surface of the mass.

The visceral nerve mass does not lie directly in front of the pedal ganglia, but partially on top of them, the two masses being closely bound together by the pleuropedal connectives and also by connective tissue.

The degree to which the visceral mass covers the pedal ganglia may be contrasted in *C. hortensis* and *C. nemoralis*. In the latter they are less superimposed, and consequently the pedal ganglia are more exposed to view than in the former (Pl. II. figs. 6 *a* and 6 *b*). The connective tissue surrounding the visceral nerve mass is often pigmented. It was found that when pigment was absent from the connective tissue of the cerebral ganglia it was also absent from that of the visceral nerve mass, and that this was also the case when the pigment on the cerebral ganglia was present but thinly distributed.

Apart from the grooves indicating the limit of the various ganglia of the visceral nerve mass, other grooves are also present, and are often intensified by a concentration of the pigment in the connective tissue above them. In *C. hortensis* these grooves tend to give the visceral nerve mass a rectangular appearance, while in *C. nemoralis* the effect is more irregular. This character, however, is very variable in each form and is of little use for diagnosis.

Genital Organs.

The genital organs of the Stylommatophora have formed the subject of a large number of investigations, and those of the Helicidae are well known. Among the important works, those of A. Schmidt, Semper, Schuberth, von Jhering, and Meisenheimer may be cited, while a full list will be found in the bibliography of Lang's 1908 paper (14).

The structure of the genital organs of *C. hortensis* and *C. nemoralis* (Pl. III. figs. 7 *a* and 7 *b*) may be ascertained from a study of Kleiner's paper, "Untersuchungen am genitalapparat von *Helix nemoralis* und *Helix hortensis*, und einer weiteren Reihe von Lang gezüchteter Bastarde der beiden Arten" (11).

Kleiner examined the genital organs of the two species with a view to ascertaining all the differences between them for purposes of comparison with those of their hybrids. Her method of measurement of a large number of forms, and subsequent treatment of the figures, form the basis of the methods employed in the present piece of work. The work on the genital organs in this paper is merely a verification of certain of Kleiner's results. She found that:

(1) The flagellum was absolutely and relatively longer, and that its variability was greater in *C. nemoralis* than in *C. hortensis*.

(2) The relation of the upper part of the receptaculum

seminis duct ("Blasenkanal" of Hesse (11)) to the lower part ("Blasenstielschaft" of Hesse) was characteristic for each form.

(3) The measurements of length of dart and dart-sac showed no overlap, and were therefore absolute criteria of species.

(4) The type of branching, and length of diverticula in the mucous glands were distinctive in the two species. The average number of diverticula on each gland was typical for each form.

Lang (14) did similar work on the flagellum, dart, dart-sac, and mucous glands. His results are in agreement with Kleiner's.

In the present investigation it was not possible to carry out all Kleiner's measurements, the flagellum and lower part of the receptaculum seminis being much coiled and too brittle in the preserved material to straighten out. The upper part of the duct of the receptaculum seminis was measured, and was found, as in Kleiner's work, to be considerably shorter in *C. hortensis* than in *C. nemoralis*, although overlap occurred in the range of variation. A similar result was obtained for measurements of the diverticulum. The length of the dart-sac was also measured. The figures will be found in Tables IV. and V.

The mucous glands were examined in about 70 animals of each species. The different arrangements found in the diverticula are given below.

Diverticula.	<i>Cepæa hortensis</i> .	<i>Cepæa nemoralis</i> .
6+4*	3.5 per cent.	—
5+5	3.5 "	—
5+4	10.4 "	—
5+3	2.3 "	—
4+4	37.2 "	3.6 per cent.
4+3	15.1 "	7.2 "
4+2	1.2 "	2.4 "
4+1	1.2 "	—
3+3	18.6 "	30.0 per cent.
3+2	3.5 "	41.0 "
3+1	—	1.2 "
2+2	—	10.8 "
2+1	—	3.6 "

This table shows that 4+4 is the most frequent combination in *C. hortensis* and 3+2 in *C. nemoralis*. This is in accordance with Kleiner for the former, but for the latter she gives 3+4. Only 7.2 per cent. of the forms examined showed this agreement.

It will also be noted that in the material examined certain arrangements of the diverticula are peculiar to *C. hortensis* and certain others to *C. nemoralis*.

This examination of the genitalia shows that the shape of the dart, and the shape and arrangement of the mucous glands may be looked upon as diagnostic characters between the two species.

* The mucous glands are paired; when one gland has six diverticula and the other four, the arrangement is expressed as 6+4.

INTER-COLONIAL VARIATION.

The figures obtained in the course of the foregoing investigation are collected in Tables IV. and V., where the mean value, standard deviation, and probable error for each organ measured are set out under the different colonies. From 30 to 60 animals from each colony were examined. These numbers are small for the type of work, but they suffice to give a good indication of the constitution of each colony.

In the last column of the tables the difference between the colony with the highest mean and that with the lowest is given for each organ. These differences were in all cases found to be statistically significant.

If the mean values for any one organ in the individuals of all the colonies are compared, it will be seen that they vary from colony to colony, and cover very much the same range in both species, except in the case of the length of the dart-sac and the length of the duct of the receptaculum seminis; i.e., except in these structures, there is no sharp distinction between the two forms in the relative size of the organs examined.

On examining the standard deviations, it is found that they are fairly constant for any one organ throughout the colonies of both species. The figures show that *Cepæa nemoralis* is, on the whole, more variable than *Cepæa hortensis*. No marked correlation is to be found between the size of the organs in any one colony.

! Some organs are noticeably more variable than others. The order of variability may alter slightly from colony to colony, but it is approximately the same throughout all the colonies in each form.

It appears from this investigation, therefore, that the colonies

Key to Abbreviations in Tables IV. and V.

m.	Mean.		
P.E.	Probable error of mean.		
d'.	Standard deviation.		
M.P.V.	Main pulmonary vein.		
F.U.	Distance from fork of vein to opening of ureter.		
L.O.N.	Distance between roots of optic nerves.		
L.C.G.	Length of cerebral ganglion.		
L.D.S.	Length of dart-sac.		
L. duct.	Length of duct of receptaculum seminis.		
L. div.	Length of diverticulum of receptaculum seminis.		
K.	Knapp Hedge Colony.	I.	Iver Colony.
C.	Chalke Bank "	N.	Nanjizal Colony.
M.	Meadow Hedge "	M.C.	Maiden Castle Colony.
H.	Hedge Lane "	W.	Wembley Colony.
S.	Suffolk "		

TABLE IV.—Mean, Standard Deviation, and Probable Error for Six Colonies of *Cepaea hortensis*.

	K.			C.			M.			H.			S.			I.			Difference between Greatest and Least Mean.
	m.	P.E.	d.	m.	P.E.	d'.	m.	P.E.	d'.	m.	P.E.	d'.	m.	P.E.	d'.	m.	P.E.	d'.	
Ventricle	17.45	.24	1.89	16.16	.27	2.09	17.07	.39	2.43	15.12	.22	1.75	13.24	.25	2.16	12.35	.18	1.83	5% approx. Significant.
Auricle	17.21	.39	2.29	13.45	.32	2.51	13.45	.31	2.47	15.54	.23	1.87	11.10	.22	1.94	10.34	.17	1.81	"
Pericardium	20.57	.33	2.63	17.86	.21	1.68	17.31	.23	1.87	17.33	.23	1.81	14.89	.30	2.56	15.10	.16	1.62	"
Kidney	37.68	.92	7.31	37.06	.87	6.94	37.06	.61	5.18	37.06	.67	5.38	31.75	.52	4.49	33.81	.51	5.32	"
M.P.V.	75.77	1.10	8.93	74.07	1.30	10.93	71.92	1.23	9.13	88.02	1.70	13.22	81.18	.90	11.46	76.68	.80	12.92	"
F.U.	56.92	1.00	8.32	46.56	.85	6.80	45.63	1.10	8.99	53.52	1.20	9.35	56.75	1.10	8.75	60.93	1.10	11.24	"
L.O.N.	18.83	.36	2.90	15.48	.21	1.94	16.82	.22	1.78	16.33	.18	1.48	14.51	.22	1.88	14.72	.24	2.48	"
L.C.G.	11.21	.27	1.71	8.73	.14	1.10	10.13	.18	1.46	8.57	.14	1.10	8.01	.07	.59	8.03	.13	1.34	"
L.D.S.	33.06	.41	3.36	27.63	.33	2.53	29.86	.39	3.03	29.54	.43	3.48	29.70	.36	3.03	27.90	.28	2.97	"
L. duct	47.02	1.20	9.15	46.10	1.10	8.55	43.42	1.30	9.92	48.34	.80	6.01	39.15	.77	6.17	31.59	.84	6.82	"
L. div.	15.74	.45	3.45	17.07	.77	6.04	13.03	.63	4.74	14.03	.55	4.12	13.61	.59	4.66	10.39	.55	4.49	"

TABLE V.—Mean, Standard Deviation, and Probable Error for Five Colonies of *Cepaea nemoralis*.

	N.			M.C.			SHATON.			W.			S.			Difference between Greatest and Least Mean.	
	m.	P.E.		d'.	m.	P.E.		d'.	m.	P.E.		d'.	m.	P.E.			d'.
Ventricle	17.25	.25	2.40	13.48	.25	2.30	15.14	.21	1.91	12.93	.16	1.50	13.25	.22	1.75	4	4 % approx. Significant.
Auricle	17.05	.30	2.80	12.32	.30	2.80	13.42	.28	2.60	12.91	.19	1.80	11.42	.26	2.10	6	"
Pericardium	25.42	.30	2.80	18.32	.19	1.80	18.06	.25	2.35	15.03	.15	1.50	17.01	.31	2.50	10	"
Kidney	43.26	.74	6.80	33.47	.50	5.20	49.80	.89	8.30	48.16	.72	6.80	40.75	.68	5.42	13	"
M.P.V.	92.85	2.10	19.20	77.47	1.40	13.30	88.64	1.50	13.70	93.47	1.59	15.40	80.96	1.60	12.10	14	"
F.U.	65.97	1.60	14.80	51.05	.83	7.70	80.95	1.16	10.02	52.19	1.00	9.70	44.57	1.20	9.60	21	"
L.O.N.	14.82	.27	2.50	14.15	.17	1.60	16.13	.29	2.60	13.57	.16	1.50	14.83	.38	2.90	3	"
L.C.G.	7.99	.15	1.40	7.73	.07	.60	7.97	.15	1.30	7.19	.07	.67	8.29	.18	1.50	1	"
L.D.S.	53.08	.63	5.80	47.30	.46	4.30	43.76	.54	5.80	43.89	.53	5.02	45.93	1.02	8.12	9	"
L. duct	92.02	2.70	25.00	61.42	1.30	11.40	80.46	1.20	10.70	79.92	2.27	20.5	60.66	1.53	11.70	32	"
L. div.	40.47	1.30	13.10	15.45	.61	5.70	33.90	1.00	9.02	27.18	1.89	17.02	19.49	.77	5.95	25	"

may vary in their mean values and range of variation. If two colonies, one from each species, are studied from this point of view, they may appear to be widely divergent, with a significant difference between the means for any one organ, or they may be so similar that it is impossible to draw a statistical distinction between them.

INTER-SPECIFIC VARIATION.

In this part of my study I have dealt with the four hundred snails which are taxonomically assigned to two different species, in virtue of differences in the shell and reproductive system, which have been mentioned on pp. 555 and 556. From mere observation no other constant differences between the two forms are apparent, and it has already been shown that the shell is not always a reliable guide. It is of interest to see whether further anatomical differences will emerge when each species is treated statistically, the same method being used as for colonial variation (p. 559).

The two hundred specimens of each group were treated as a sample of the total population of their respective "species." In Table VI. the calculated mean, standard deviation, and probable error of the above-mentioned eleven measurements are set out, and the significance of the difference between the means of the two forms is calculated. It will be seen that the difference in mean size for the pericardium, kidney, pulmonary veins, distance between the roots of the optic nerves, dart-sac, and duct and diverticulum of the receptaculum seminis appears to be significant.

From the study of inter-colonial variation in each group, however, it will be seen that the statistical characters of the "species sample" must depend on the character of the colonies of which it is composed. It has been shown that the colonies vary markedly from one another: it is therefore obvious that, to ascertain how far the aggregate of individuals diagnosed as "*nemoralis*" or "*hortensis*" on the characters of the shell and genitalia differ also in the other characters under consideration, it would be necessary to collect a "good sample" (2) of material from a large number of colonies distributed all over the geographical range of the two forms. This, however, does not deprive the data here represented of their value as expressing the average obtained from several distinct colonies, and therefore giving some approximation to the characters of the *C. hortensis* and *C. nemoralis* populations of the area from which the colonies were obtained. It must be understood that the differences set forth in the tables are those found in the particular sample under consideration; and though the colonies from which the individual specimens were taken are widely separated from each other, it must not be assumed that the differences in question are characteristic of the whole *Cepæa* population.

TABLE VI.

	<i>Cepaea hortensis.</i>			<i>Cepaea nemoralis.</i>			Significance.		
	Mean.	P.E.M.	d'.	Mean.	P.E.M.	d'.	Diff.M.	P.E.D.	Significance.
	%			%			%		
Ventricle	14.9	.13	2.8	14.46	.12	2.4	.44	.2	—
Auricle	18.17	.15	3.2	18.53	.15	3.1	.36	.2	—
Pericardium ...	18.97	.14	2.9	18.96	.21	4.2	1.99	.2	Sig.
Kidney	34.93	.29	6.2	40.99	.39	8.0	6.06	.5	„
M.P.V.	77.5	.6	12.5	87.12	.82	16.5	9.62	1.0	„
F.-U.	54.37	.5	10.5	55.27	.64	12.8	.9	.8	—
L.O.N.	15.95	.12	2.6	14.66	.12	2.4	1.29	.1	Sig.
L.C.G.	8.69	.08	1.7	7.79	.08	1.2	1.1	.1	—
L.D.S.	29.45	.17	3.5	47.12	.33	6.6	17.67	.4	Sig.
L. duct R.S. ...	42.0	.51	9.6	69.92	1.05	20.9	27.92	1.1	„
L. div. R.S. ..	13.78	.27	5.2	27.42	.73	14.4	13.64	.8	„

P.E.M. Probable error of mean.

Diff. M. Difference between means.

P.E.D. Probable error of difference.

d'. Standard deviation.

M.P.V. Main pulmonary vein.

F.-U. Distance from fork to ureter.

L.O.N. Distance between roots of optic nerves.

L.C.G. Length of cerebral ganglion.

L.D.S. Length of dart-sac.

L. duct R.S. Length of upper part of duct of receptaculum seminis.

L. div. R.S. Length of diverticulum of receptaculum seminis.

SUMMARY.

1. Two sets of individuals diagnosed on the characters of shell and genitalia as *Cepaea hortensis* and *Cepaea nemoralis* have been examined. Each set was obtained from colonies in Wiltshire, Devonshire, Cornwall, Suffolk, Buckinghamshire, and Middlesex.

2. The following structures were examined: pulmonary vessels, genitalia, kidney, heart, pericardium, and nervous system.

3. The measurements obtained are presented as they relate to :

- (a) the differences between the colonies of each species ;
- (b) the differences between the species as currently designated.

4. The only absolute distinctions in internal anatomy between the species *C. hortensis* and *C. nemoralis* as recognized by the shell-characters are :

- (a) the shape of the dart ;
- (b) the arrangement of the mucous glands.

5. The colonies of each species may differ significantly from one another, when the individual characters are treated statistically.

6. It is probable that a sample drawn from a few colonies only, even though it contain a large number of individuals, is of little value for the determination of the characters of a larger population.

The differences found, however, are valid for the section studied, and it may be that they represent definite differential tendencies in the population as a whole, which might be correlated with the shell-characters.

7. Certain organs show a wider range of variability than others: *e.g.*, the pulmonary vessels, genitalia, and kidney are markedly more variable than the heart, pericardium, and nervous system.

8. The order of variability of the organs is almost identical in the two species and in their colonies.

9. The various organs do not show the same amount of divergence when those of the one population sample are compared with those of the other. Thus there is more marked divergence between the length of the dart-sac of "*nemoralis*" individuals and that of "*hortensis*" individuals than there is between the kidney of the two groups. The following list gives the order (from greatest divergence to least) in which such divergence is manifested in the two samples:—

Length of duct of receptaculum seminis.

Length of dart-sac.

Length of diverticulum.

Length of main pulmonary vein.

Length of kidney.

Pericardium.

Distance between optic nerves.

10. The organs in *C. nemoralis* are, on the whole, more variable than those in *C. hortensis*

Explanation of Abbreviations used in Table VII.

L.v.	Length of ventricle.
L.a.	Length of auricle.
L.k.	Length of kidney from pericardium to apex.
W.pc.	Width of pericardium.
K.-f.	Length of main pulmonary vein from apex of kidney to main fork.
F.-n.	Distance from main fork of pulmonary vein to external opening of ureter.
L.o.n.	Distance between roots of optic nerves.
L.G.	Length of cerebral ganglion
M.G.	Mucous glands.
L.d.s.	Length of dart-sac.
B.d.s.	Breadth of dart-sac.
L.d.	Length of "Blasenkanal."
L.div.	Length of diverticulum.
Cor.	Corrected figures.

Specimen Table showing method of tabulating measurement.
TABLE VII.—*Cepaea nemoralis*. Wenbley.

Number of Specimen.	Height of Shell.	I.v.		L.a.		L.k.		W.pc.		K.f.		F.u.		L.G.		M.G.	L.d.s.		B.d.s.		L.d.		L.div.	
		%	Cor.	%	Cor.	%	Cor.	%	Cor.	%	Cor.	%	Cor.	%	Cor.		mm.	Cor.	mm.	Cor.	%	Cor.	%	Cor.
W 1	14	14.3		14.3		42.9		14.3		68		53.6		14.3		3+3	6.5		3		57.2		8.9	
W 2	14	12.5		12.5		44.6		14.3		83		50		14.3		3+2	6.5		3		60.8		21.4	
W 3	14	10.7		10.7		39.3		14.3		85.5		48.5		14.3		3+2	6		3		89.3		14.3	
W 4	14	10.7		10.7		53.6		14.3		96.5		46.5		14.3		3+2	5.5		3		53.6		14.3	
W 17	14	14.3		14.3		50		14.3		93		68		12.5		2+2	5.5		2.5		103.6		53.6	
W 18	14	14.3		14.3		50		14.3		100		60.8		14.3		3+1	6		2.5		82.2		21.4	
W 19	13.5	12.9		14.8		37		14.8		77.5		52		14.8		2+3	7		2.5		92.6		33.4	
W 20	14.5	13.8		13.8		51.7		15.5		75.7		55.2		12.1		3+2	—		—		67.3		25.9	
W 24	14	14.3		17.8		46.4		17.9		78.7		53.5		14.3		2+2	7		3		85.7		16.1	
W 29	14	14.3		10.7		42.9		14.3		64.5		46.5		14.3		2+2	7		3		—		—	
W 30	14	14.3		14.3		32.1		17.9		112.5		50		14.3		3+2	5.5		3		42.8		14.3	
W 31	14	12.5		14.3		42.9		14.3		112.5		28.6		10.7		3+2	6		3		—		—	
W 32	13.5	14.8		14.8		40.7		14.8		100		59.3		14.8		2+2	6.5		3		96		59.3	
W 33	14	14.3		10.7		39.3		14.3		85.5		57.2		14.3		3+3	5.5		3		—		—	
W 34	16	12.5		12.5		43.8		12.5		75		62.5		12.5		3+3	6		3		81.2		87.5	
W 35	14.5	13.8		10.3		44.9		17.2		65.6		62.2		13.8		3+2	7.5		3		110.4		62.2	
W 37	15	13.3		13.3		50		13.4		93.5		60		13.3		3+2	6		2.5		101.7		11.7	
W 38	14	12.5		14.3		55.4		14.3		83		53.5		14.3		3+3	6.5		3		91		21.4	
W 39	15.5	9.7		12.9		38.8		14.5		113		51.7		12.9		2+1	6		3		71		12.9	
W 41	14	14.3		14.3		57.2		16.1		103.8		50		10.7		3+3	—		—		76.5		23.6	

W 42	14	14.3	14.3	42.8	17.9	100	39.3	14.3	7.1	3+2	6.5	3	71.4	16.1
W 43	14	12.5	14.3	57.2	14.3	96.5	46.5	14.3	7.1	3+2	8	3	82.2	28.6
W 44	15.5	9.7	9.7	38.8	13.3	64	45.2	12.9	6.4	3+2	6.25	2.6	64.5	19.4
W 45	13.5	14.8	12.9	55.6	14.8	77.8	37	13	7.4	4+3	6	2.5	103.3	22.2
W 49	14	10.7	10.7	41.1	16.1	107.4	44.7	14.3	7.1	2+2	6	2.5	69.6	17.9
W 50	13	12.9	12.9	36.6	15.4	115.4	65.5	13.5	7.6	2+2	6	2.75	—	—
W 51	14	10.7	12.5	42.8	14.3	111.0	46.5	14.3	8.9	(2+2)+3	6.5	3	82.2	28.6
W 52	13.5	14.8	11.1	44.5	18.5	85.2	57.5	14.8	7.4	3+3	6.5	2.5	44.5	14.8
W 53	14	10.7	10.7	41.1	14.3	103.6	26.8	14.3	8.9	3+3	6	3	—	—
W 54	15	13.3	13.3	53.4	16.7	110.0	40	13.3	6.7	3+2	6.5	3.5	100	23.4
W 55	15	13.3	13.3	53.4	13.3	103.4	60	13.3	6.7	2+1	8	3	116.8	58.4
W 56	15	13.3	13.3	46.7	16.7	86.7	46.7	13.3	8.3	2+3	5.5	2.75	53.4	15
W 57	14	14.3	10.7	46.5	14.3	107.1	62.5	14.3	7.1	2+3	6	3	64.3	28.6
W 58	14	14.3	17.8	41	17.9	114.3	39.3	14.3	7.1	3+3	6.5	3.25	60.7	28.6
W 59	14.5	12.1	12.1	44.9	13.8	103.2	55.2	10.3	6.9	3+3	5.5	2.55	—	—
W 61	15.5	12.9	12.9	48.4	16.1	100	54.8	12.9	6.5	2+3	6.5	3	98.5	19.4
W 62	12	12.5	12.5	56.3	16.7	100	62.5	—	—	3+2	5.5	2.5	125	50
W 63	14	12.5	12.5	46.5	14.3	85.7	60.7	16.1	7.1	3+2	6	3	78.5	17.9
W 64	14	14.3	14.3	42.8	14.3	107.1	46.5	17.8	10.7	3+2	6	3	76.8	19.7
W 65	14	10.7	10.7	46.5	10.7	88.9	42.8	10.7	7.1	2+2	6.5	3	57.2	35.7
W 68	14	14.3	12.5	42.8	14.3	64.3	60.7	14.3	7.1	3+3	6.5	3	82.2	28.6
W 69	14	14.3	14.3	53.6	14.3	110.6	67.9	10.7	7.1	2+1	6	2.5	114.4	21.4
W 70	15	13.3	13.3	65	16.7	96.7	46.7	11.7	6.7	3+3	7	3	83.4	15
Total 43.	—	560.6	558.2	991.8	646.6	3998.5	2222.9	569.8	303.1	—	—	—	2994.8	1016.5

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EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1 a. Anterior part of the roof of the lung of *C. hortensis*, from the inside. $\times 52$.

A. Anus. A.P.V. Afferent pulmonary vein. E.P.V. Efferent pulmonary vein. G.U. Ureter groove. K. Apex of kidney. M.E. Edge of mantle. M.L. Mantle-lobe. O.U. Opening of secondary ureter to exterior. P. Pneumostome. R. Rectum. R.L. Roof of lung. U. Primary ureter.

Fig. 1 b. Posterior part of the roof of the lung of *C. hortensis*, from the inside, showing heart and kidney. $\times 96$.

A. Auricle. O.P. Opening of secondary ureter to form a groove. P. Pericardium. S.U. Secondary ureter. V. Ventricle.
Other letters as in fig. 1 a.

PLATE II.

Fig. 3. Alimentary canal of *C. nemoralis*. $\times 64$.

A. Anus. B.G. Right buccal ganglion. C. Crop. C.B. Right cerebro-buccal commissure. Co. Cæcum. D.S. Duct salivary gland. E. (Esophagus. H. Entrance of hepatic ducts to stomach. I. Intestine. P.B. Pharyngeal bulb. P.M. Line of attachment of retractor-pharynx muscle. R. Rectum. R.S. Radula sac.

Fig. 4. Jaw of *C. nemoralis*. $\times 196$.

R. Ridges.

Fig. 5 a. Cerebral ganglia of *C. nemoralis* before removal of connective tissue. $\times 16$.

C. Cerebro-pleural and cerebro-pedal connectives. O. Optic nerve. P. Penis nerve. Pr. Protocerebrum.

Fig. 5 b. Cerebral ganglia of *C. hortensis* before removal of connective tissue. $\times 16$.

Ch. Cerebro-buccal connective. C.p.d. Cerebro-pedal connective. C.p.l. Cerebro-pleural connective. O. Left optic nerve. P. Penis nerve. Pr. Protocerebrum.

Fig. 5 c. Cerebral ganglia of *C. hortensis* with connective tissue removed. $\times 16$.

C. Cerebral commissure. M.C. Mesocerebrum. M.t.c. Metocerebrum.
Other letters as in fig. 5 b.

Fig. 6 a. Pedal ganglia and visceral mass of *C. nemoralis* with connective tissue removed. $\times 16$.

A. Anal nerve. C. Cutaneous nerve. C.P.D. Cerebro-pedal connective. C.P.L. Cerebro-pleural connective. L.P. Left pallial nerve. L.Pa. Left parietal ganglion. R.Pa. Right parietal ganglion. R.P.C. Right pedal ganglion. R.P. Right pallial nerve. V. Visceral ganglion. Vis. Visceral nerve.

Fig. 6 b. Pedal ganglia and visceral mass of *C. hortensis* with connective tissue removed. $\times 16$.

P.L. Left pleural ganglion.
Other letters as for fig. 6 a.

PLATE III.

Fig. 7 a. Genital organs of *C. hortensis*. $\times 22$. After Hesse.

A. Atrium. Al. Albumen gland. B.K. "Blasenkanal." B.S. "Blasensteinschaft." C.D. Common efferent duct. D. Diverticulum. D.S. Dart-sac. F. Flagellum. H. Hermaphrodite duct. M.G. Mucous glands. P. Penis. R.P. Retractor penis muscle. R.S. Receptaculum seminis. V. Vagina. V.D. Vas deferens.

Fig. 7 b. Genital organs of *C. nemoralis*. $\times 22$. After Hesse.

Letters as for fig. 7 a.

PLATE IV.

Diagrams of types of branching of efferent pulmonary vessels found in *C. hortensis* and *C. nemoralis*.

M.P.V. Main pulmonary vein. M.F. Main fork of pulmonary vein.

37. The Resistance of Certain Metals and Metallic Alloys to Corrosion and Solution by Sea-Water. By FLAXNEY PERCIVAL STOWELL, B.Sc., Ph.D., A.I.C., Aquarium Research Fellow.

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The corrosion and solution of metals by sea-water is one of the most important of present-day problems confronting the metallurgist. The reason is not far to seek. Since metals, notably iron, are essential in the construction of ocean vessels and liners, piers, harbour structures and docks, and all the metals at present in use for those structures are more or less attacked by sea-water, continuous research has been and is being conducted on the various problems of corrosion, with a view to lessening the expense and inconvenience caused by it, and to producing, if possible, an alloy which will withstand the attack of sea-water, or, failing that, a protective paint or varnish which will render the metal immune. The literature on the subject is so immense that no attempt is made here to compile general references; the reader is referred to standard works on the corrosion of metals (1).

The solvent and corrosive action of sea-water on metal fittings is a problem which also confronts the aquarist. Though corrosive action is a matter of great concern, the solvent action of a water also restricts the aquarist in the choice of metallic fittings for his show-tanks and circulatory apparatus. This is on account of the fact that fish are particularly susceptible to minute traces of the heavy metal ions in the water they inhabit, very small concentrations being toxic. It is stated by Marsh (2) that the minimal fatal concentration of copper ion, for instance, is one part in 6.5 millions of water. The ions of silver and lead are also very toxic. Hence, though the limiting fatal concentration must necessarily vary, depending on the size and kind of fish, the rate of flow of the water, its oxygen-content, and many other factors, it is necessary, in order to be absolutely safe, either to limit the choice of metal for fittings to one which, though susceptible to attack by sea-water, is non-toxic in the ionic condition to fish, or to employ an alloy or protective coating which is non-corrosive. Since, up to the time of the construction of the Society's Aquarium, no non-solvent or corrosive alloy was obtainable at a reasonable cost, the main portion of the metallic fittings in the sea-water circulation were made of iron, which, although corrodible by and soluble in sea-water, is non-toxic in relatively small concentrations to fish-life. Copper and zinc fittings were avoided, for although the corrosion by sea-water is less than in the case of iron, the metals in solution are much more toxic.

Cast iron, however, though certainly the best and cheapest of the known materials for piping and other fittings in the Aquarium,

leaves much to be desired, on account of the accumulation of rust, which tends to block up working parts, and in time renders necessary the replacement of fittings. It is also extremely inconvenient, in fact almost impossible, to employ iron for all the fittings. Before any other metal or alloy can be used, exhaustive tests are necessary in order to ascertain the corrosive effect of sea-water under the working conditions, and to estimate the amount of metal which passes into solution.

Corrosion-resisting metals usually owe their properties, according to Evans (3), either to their *low* affinity for oxygen, or to their *very high* affinity for the element. In the first class may be placed the noble metals, platinum, gold, and silver. Their cost, however, renders their use in large quantities prohibitive. In the second class are metals and alloys which readily become covered with a protective coating of oxide, which renders them practically immune from further attack. The action of the surrounding medium will continue until a protective coating forms on the metal; if no coating forms, the action will continue indefinitely. If this is the case when the metal is immersed in sea-water, it is clearly useless to employ it for fittings, if the metal in the ionic condition is toxic to fish-life, unless an artificial protective coating be applied, such as a paint or varnish. In some cases a coating may be induced chemically by the addition of some constituent to the water, such as the silicate coating induced on lead, mentioned in a later section of this paper.

Various investigations have been carried out by the author on the corrosion and solution by sea-water of metals, alloys, and protective paints in connection with necessary fittings in the Aquarium circulation, in order, if possible, to find an ideal non-corrosive metallic alloy for the purpose, or, if that were impracticable, to induce the formation of a protective coating which would successfully withstand the action of the sea-water. The results are embodied in the following paper, which is not intended to be a systematic investigation of corrosion by sea-water, but rather a practical survey of the action of sea-water on certain of the well-known metals, alloys, and protective paints. Some cases, such as copper and zinc, have not been examined in any detail, as it must be remembered that for aquarium purposes the amount of metallic ion passing into solution is of great importance. If one of the products of corrosion is soluble in water, and the metallic ion is toxic to fish-life, the practicability of the metal is nil, and further investigation useless.

Lead.

Lead is dissolved by most soft waters; that is, waters containing little carbonate and bicarbonate, especially if the water contains organic acids. But hard waters with small free carbon-dioxide content have very little action, as the metal becomes covered with a coating of lead oxycarbonate. More free carbon-dioxide present retains the lead carbonate in solution. According to Friend and Tidmus (4), the presence of chlorides and nitrates increases the corrosion, while sulphate depresses it.

Sea-water contains a large amount of carbonates and bicarbonates, and is alkaline. Chlorides are present in high concentration in sea-water, but their effect is to a certain extent neutralised by the presence of sulphates. It is not to be anticipated, however, that sea-water, being hard and alkaline, will have a high solvent action on lead.

Sample strips of chemically pure lead, ordinary commercial lead, and a lead-tin alloy, of practically identical weight and surface-area, were thoroughly cleaned and totally immersed in separate portions of 100 c.c. of sea-water of p_H 8.0 and temperature 16° C. Every twenty-four hours the water was withdrawn and carefully washed into Nessler cylinders, and the amount of lead present estimated by the sulphuretted hydrogen method, by which one part of lead in ten million parts of solution is detectable. The samples were then replaced in fresh sea-water, without disturbing any protective coating which had formed. A duplicate set of strips were immersed under similar conditions in sea-water to which had been added sodium silicate in the concentration of one grain per gallon of sea-water (5).

The untreated lead samples changed very little in appearance during the experiment, a slight tarnish appearing on the surface, but no local corrosion or pitting was observable. In the case of the pure lead, traces of a white powder were found on the bottom of the containing vessel after three days. This powder consisted of lead carbonate and chloride. After three or four days, the samples under silicate treatment became covered with a strong coating, of greyish-white appearance. Again no local corrosion could be detected.

Table I. gives the amount of lead expressed in parts per ten million of solution estimated at the end of each twenty-four hours. Column (5) in the table shows the amount of solution from a strip of pure lead immersed in London tap-water, in order to afford a comparison with the solution in sea-water.

TABLE I.

Duration of expt. in days.	Pure lead sample.	Commercial lead sample.	Lead-Tin Alloy.	Pure lead in fresh water.	Pure lead, silica treated.	Comm. lead, silica treated.
1 . . .	10-15	8	7	40	10-15	10-15
2 . . .	7	7	6	12	10	10-15
3 . . .	5	8	5-6	7-8	7	8
4 . . .	5	7	5	7	5	5
5 . . .	6	6	6	7	4	3
6 . . .	5	(12)	(10)	7	3	3
8 . . .	4	2-3	5-6	8	2	2
8 . . .	3-4	4	5-6	7	2	1
10 . . .	3-4	1-2	3-4	4	* < 1	< 1
11 . . .	3-4	1-2	3-4	5	< 1	< 1

* Limiting minimal amount detectable.

In the case of each sample immersed in sea-water, an appreciable amount of lead had gone into solution each day, the amount gradually decreasing. At the end of eleven days, however, solution was still apparent. The solvent action of the sea-water is less than that of the fresh water of hardness 19°. The samples immersed in sea-water containing sodium silicate also showed solution at the commencement, the amount passing into solution decreasing steadily as the protective coating of lead oxysilicate formed, until at the end of ten days the samples were practically immune from further attack.

As a result of the investigation, the lead coils of a refrigerator which had just been included in the sea-water circulation of the Aquarium were allowed to soak for ten days in sea-water containing sodium silicate in the concentration of one to two grains per gallon. At the end of this period it was found that a uniform coating of lead oxysilicate had formed on the coils, and though the refrigerator has now been in use for eighteen months, no sign of corrosion or solution of the lead is detectable.

Zinc and Zinc Alloys.

It is only to be expected that zinc will be corroded by sea-water, as zinc chloride and zinc sulphate are both soluble salts. A sample of zinc totally immersed in sea-water displays local corrosion in the form of white points of zinc hydroxide, which gradually stream down the surface if the sample strip be supported vertically, forming a gelatinous mass at the base of the strip. Appreciable quantities of zinc pass into solution. Semi-immersion causes corrosion at points halfway down the strip, from which zinc hydroxide streams downward. Corrosion also takes place at the base of the strip, and gradually spreads upwards till eventually the sample is completely eaten through. It is obvious, therefore, that zinc is totally unsuitable for fittings in contact with sea-water.

Copper.

The action of sea-water on copper has been exhaustively investigated by Bengough and May (6). According to them, cuprous chloride is first formed when sea-water acts on copper, this in turn being oxidized to cupric chloride and oxychloride. Copper carbonate and hydroxide are also formed. An appreciable solution of copper consequently takes place, which, owing to the toxic nature of the copper ion, furnishes a sufficient reason for its exclusion from the list of metals suitable for aquarium fittings.

An important alloy of copper and nickel is known commercially as *Monel Metal*. This has a fairly resistant action to sea-water, but on account of the copper it contains, it must be considered as unsuitable for the present purpose. In contact with steel, moreover, intense corrosion of the latter occurs (7).

Aluminium.

Little work has been done on the toxicity of the aluminium ion to fish life, consequently the approximate minimal fatal concentration is not known. The degree of corrosion of aluminium in natural waters depends to a great extent on its purity. Seligman and Williams (8) find that hard water containing calcium bicarbonate, sulphates, and chlorides produces a localized corrosion in aluminium, known as "blistering." Though aluminium tends to become covered with a protective film, the presence of chlorides causes a breakdown in the film. Since sea-water contains bicarbonate of calcium, sulphates, and chlorides, the action on aluminium will be analogous to that described by Seligman and Williams (*loc. cit.*). It is certain that aluminium chloride will pass into solution, the salt being very soluble in water; hence the suitability of aluminium for our present purpose, apart from the aspect of localized corrosion, is limited by the lack of accurate knowledge as to the relative toxicity of the aluminium ion.

Iron.

Since the corrosion of iron is a problem which has been investigated more extensively than that of any other metal, and the literature on the subject voluminous, it is unnecessary to go into great detail in the present paper. For a review of the problem, the reader is referred to U. R. Evans's 'Corrosion of Metals' or other standard work. Solutions containing sodium chloride readily attack iron, the anodic product of corrosion being ferrous chloride and the cathodic product sodium hydroxide. Ferrous hydroxide is precipitated, and this is rapidly oxidized to ferric hydroxide and ferri-ferroso hydroxide. The presence of wet rust promotes further corrosion.

The use of sodium silicate has been recommended to retard the corrosion of iron pipes by water. Evans (9) has found, however, that the presence of chlorides reduces the protective action, and if the silicate is present in small quantities, local corrosion still occurs. Since silicate treatment had been found so effective by the author in the case of lead, samples of pure iron in the form of strips were submitted to a similar treatment; viz., total immersion in sea-water containing sodium silicate in the concentration of one grain per gallon. Though the total corrosion was slightly reduced, local corrosion and pitting took place.

Corrosion-resisting Steels.

In the present series of investigations most attention has been devoted to the action of sea-water on resistant steel alloys, since it is possible to neglect the small amount of iron which passes into solution, on account of its non-toxicity to fish-life, and to concentrate on the aspect of corrosion pure and simple.

Most of the corrosion-resisting or "stainless" steels are steels containing varying proportions of chromium or nickel, or both.

These alloys readily form a protective coating or film of oxide on their surface, which renders the underlying layer immune from attack. The point arises, however, as to how far the film of oxide is continuous and adherent, especially when immersed in a liquid like sea-water, which contains chlorides, sulphates, and carbonates, all of which may cause a break in that continuity. Again, whereas a corrosion-resisting alloy may withstand attack at all points if totally immersed, it has been found that the resistance may break down at the water-line if the alloy is only partially immersed. Hatfield (10) states that 14 per cent. chromium steel is attacked at the water-line if partially immersed in sea-water.

The action of sea-water on one of the best of these corrosion-resisting steels, which is known commercially as "Staybrite," was closely investigated by the author. The steel contains chromium and nickel. It is resistant to phosphoric, acetic, formic, and tartaric acids, and even to concentrated nitric acid, and it is claimed that it can be welded.

The samples were submitted to the most rigorous tests. Two cylinders of the steel were suspended by silk threads in sea-water of p_H 7.9 and temperature $29^{\circ}C$. Minute air-bubbles entering from the base of each container impinged on the cylinders, in order to reproduce as far as possible the conditions under which metallic fittings are subjected to contact with agitated, well-aerated sea-water. Loss of solvent by evaporation was made up each day with distilled water, and the iron-content of the sea-water determined before and after the experiment, which lasted a month. Plates of the metal were also semi-immersed in sea-water at the same temperature. One of these strips had been cut into two pieces in order to expose a freshly-cut surface to the sea-water.

At the end of a month no corrosion or pitting was observable in either of the totally-immersed specimens. The water containing them was analysed and found to contain only 0.0024 grammes of iron per litre. The plates subjected to the semi-immersion test displayed very slight corrosion at the water-line at the end of a month, with slight pitting. In the case of the freshly-cut semi-immersed plates, however, corrosion had started at the end of a week, in each case at the air-water interface, at the point where the freshly-cut surface was exposed, and in a fortnight had spread over the whole water-line. This gradually extended down each plate till rust was observable in streaks from the air-water interface to the bottom of the plate. The bottom of the containing vessel was covered with rust.

It appears, therefore, from the results obtained, that this steel, like all other chromium or chromium-nickel steels, owes its resistant properties to the formation of a thin oxide film, which is continuous and adherent. This film withstands the attack of aerated sea-water extremely well if totally immersed; and even if submitted to the more exacting test of semi-immersion, is

much more resistant than any other metal or metallic alloy examined.

Evans (11) has shown that currents are set up between parts of an iron surface by differences in oxygen concentration caused by the presence of rust. Consequently, the appearance, in the case of the freshly-cut specimens, of the products of corrosion at a particular point promotes further corrosion, on the principle of differential aeration. Hence it is advisable, if this alloy be employed for pipes, fittings, or structures in contact with sea-water, to allow some period to elapse after cutting or working the material, before submitting it to contact with the water, in order to allow the natural protective film of oxide to reform on the freshly-cut or scratched surfaces. If this precaution be taken, there is no doubt that "Staybrite" will withstand the corrosive action of sea-water quite creditably.

Protective Paints, Varnishes, and Bituminous Mixtures.

By far the cheapest and most convenient method of attempting to minimize corrosion is the application of a protective coating of paint or varnish. An ideal coating is naturally one which is impervious to water and which is continuous. Paints contain, amongst other constituents, a drying oil (such as linseed oil), which is converted in air into a solid layer, and a pigment, which hardens the drying oil. The weaknesses of most paints seem to lie in the failure of the pigment to prevent cracking in the layer formed by the drying oil. Moreover, unless the surface to be treated is smooth and dry, and the spreading of the paint very carefully executed, pinholes occur on drying. These are the cause of intense local corrosion. Bituminous layers also tend to form pinholes if badly spread. Samples of iron coated with various varnishes and bituminous mixtures were submitted to total and semi-immersion tests in sea-water at 18–25° C., and in every case local corrosion and pitting was observable, presumably at a crack or pinhole pocket formed on drying. The total corrosion was, of course, smaller than in the case of the unprotected iron, but was very intense locally. Samples immersed in sea-water and impinged on by a jet of minute air-bubbles, quickly broke down at the points of contact with the air; in fact, in some instances, whole fragments of the protective coating had been torn away. Details of each experiment are not given, as the general result only is relevant; namely, that protective paints and bituminous tend to pit badly when immersed in aerated sea-water. The fault may not lie in the paint so much as in the manner of applying. It must be borne in mind that it is practically impossible in most cases to prepare the metal to be painted so carefully that the coating "wets" the surface completely; and, in consequence, intense corrosion occurs in the minute crevices which are left unprotected, and to which the sea-water has access.

Conclusions.

Though, as already stated, the present paper is not supposed to be a systematic investigation of corrosion by sea-water, the results described bring out one or two salient facts, which are in line with well-known corrosion theories. The resistance to corrosion of the less noble metals and alloys is due to the formation of a protective coating. For complete immunity from attack this coating must be continuous and adhesive, and must also be non-soluble in, and non-permeable by, the liquid medium causing the corrosion. This coating may be induced naturally; that is, as a result of the formation, on the surface of the metal, of oxide, or of the products of reaction between the metal and the surrounding medium. As an example of this may be cited the resistant steel alloy, "Staybrite," which, as the results show, owes its resisting powers to the formation of a thin but adherent and impervious oxide film.

If this protective coating is not formed naturally, such as by atmospheric oxidation, it is sometimes possible to induce it by chemical treatment. The reaction between lead and silica, present in solution as sodium silicate, results in the formation of a more or less adherent and continuous coating of lead oxysilicate, which renders the metal immune from further attack.

Finally may be mentioned the artificial production of a protective coating, such as the application of a paint or varnish. The difficulties presented in obtaining a perfect coating are twofold—assuming a perfect paint or enamel, impervious and resistant to sea-water, the problem remains of its application to metal fixtures without the formation on drying of minute cracks and pinholes.

The value of semi-immersion as a more rigorous and exacting test than total immersion was suggested to the author by Mr. U. R. Evans, of King's College, Cambridge, and is abundantly justified by the results obtained, as samples which successfully withstand total immersion very often break down on semi-immersion at the air-water interface. In practical tests, therefore, unless the material is specifically intended for completely submerged fixtures, it is always advisable to carry out semi-immersion as well as total-immersion tests.

SUMMARY.

1. A brief account is given of various tests relating to the corrosive and solvent action of sea-water on metals and metallic alloys.

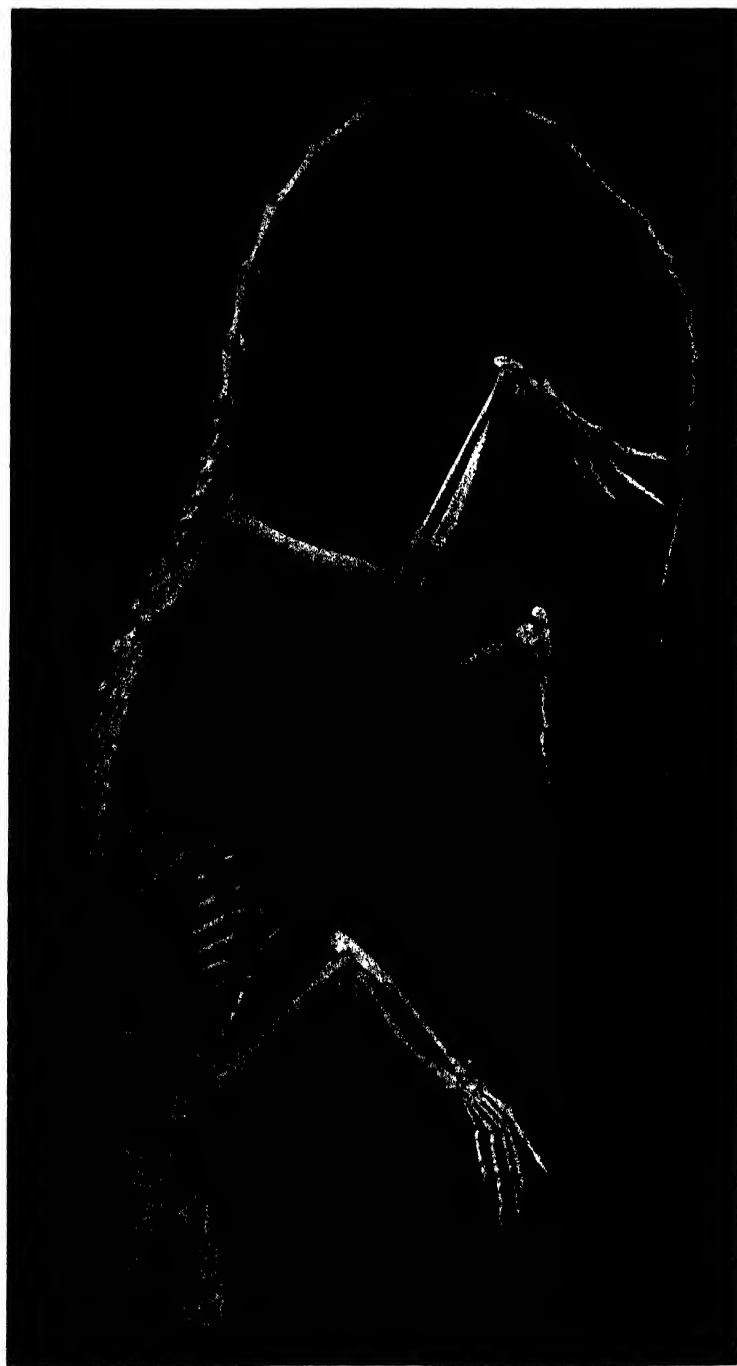
2. Natural films of oxide or chemically-induced protective coatings have been found in two cases to withstand fairly successfully the attack of sea-water.

3. The weakness of paints and varnishes as protective coatings lies in the formation of minute cracks and pinholes, which cause pitting when brought into contact with sea-water.

4. Semi-immersion was found to be a more rigorous and exacting test than total immersion, and test samples should be submitted to both treatments before an opinion is expressed as to their corrosion-resisting properties.

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THE SKELETON OF *HAPALE JACCHUS*.



A.



B.



C.

PHOTOMICROGRAPHS OF HAIRS FROM
(A) *HAPALE*. (B) *GALAGO*. (C) *TARSIUS*.

38. The Anatomy of the Common Marmoset (*Hapale jacchus* Kuhl). By J. BEATTIE, M.D., M.Sc., C.M.Z.S., Anatomist to the Society, and Demonstrator of Anatomy, University College, London.

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(Plates I. & II.; Text-figures 1-39.)

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INTRODUCTION.

The preparation of a complete monograph on the anatomy of the Marmoset (*Hapale jacchus* Kuhl) was undertaken at the request of Professor Elliot Smith with the object of settling the affinities of the primitive Platyrrhiniæ to the Eocene Tarsioids. The Marmoset was chosen because the brain of this animal showed several points of resemblance to that of the living *Tarsius spectrum*, and also because a large number of specimens of the animal could be obtained with ease.

The choice of the animal may not commend itself to those who regard the Hapalidæ as aberrant members of the Platyrrhinæ and as extremely specialised animals. It is true that in their method of progression the Hapalidæ differ considerably from other Primates; but, as will be shown later, this modification has taken place relatively late in the history of the group, and affects but little the basic primitive characters of the animals. The opinion of some observers that the Hapalidæ are the most primitive of all the Primates and are closely related to some primitive unguiculate ancestor, has been based almost entirely on the presence of claws which are found on all the toes and fingers with the exception of the hallux. This view has been regarded as erroneous by Gregory (1920). He regards the Hapalidæ as specialised Platyrrhine Monkeys.

Huxley (1876) and Macalister (1878) separated the Marmosets from the Cebidæ, and grouped them as the *Arctopithece*. Huxley's reason seems to have been based on the fact that he could not regard them as truly belonging to the *Quadrumanæ* (the fore-foot "is a mere paw, and the term 'hand' is not applicable to it"; the plantar surface of the hind-foot "is very long, and the digits are very short. It follows from these facts that the term 'quadrumanous' is not applicable in any sense to the Marmosets").

In a monograph of this kind, where the terms primitive, specialised, generalised, and advanced are used frequently, it is important to recognise the exact meanings of these words, as an improper use of them has led to many misunderstandings in the past. One cannot do better than adopt the definitions given by Todd. The words are used in this paper to express the meanings he has given.

A primitive animal is one which has retained many of its ancestral or archaic characters. It may be specialised, but cannot be generalised, nor can it be advanced. A generalised animal may be primitive, and usually is, in some respects. It is not specialised, because it retains the ability to change its life-habits with changing environment. The advanced animal cannot be primitive, but it may be either generalised or specialised. It is an animal which has changed greatly from its ancestral type. The specialised animal may be primitive or advanced, but it is an animal which has lost its power of adaptation to changing environment, and is therefore not generalised.

A perusal of this paper will, I think, tend to establish the proper relations of the Hapalidæ. It will give my reasons for believing that the Marmoset is a basically primitive primate.

This paper is based entirely on personal observation except where duly acknowledged. Dr. H. H. Woollard undertook the investigation of the central nervous system. He has allowed me to use his specimens of the eye of the Marmoset in writing the section on the eye in this monograph. I am indebted to him

for allowing me to use his conclusions on the brain of the animal to complete my review of its affinities.

Mr. F. Martin Duncan has prepared notes on the structure of the hair, and has compared it with that of *Tarsius* and other South American Monkeys. I wish to express my thanks to Dr. Woollard and to Mr. F. Martin Duncan for their assistance.

I have to acknowledge the continual encouragement and advice given to me by Professor G. Elliot Smith. He has displayed great interest in the work, and has helped me by placing at my disposal obscure papers which I could not have obtained otherwise.

I wish to express my thanks to Mr. T. L. Poulton for the pains he has taken to produce the accurate and beautiful illustrations for this paper. All the illustrations have been drawn by him from the original preparations.

MATERIAL.

Fourteen animals were available for study. Ten of these had been eviscerated and preserved by my predecessor, the late Dr. Sonntag. The remaining four were obtained fresh. Two were dissected in the fresh state and the others preserved for histological investigation. One specimen of a *Midas geoffroyi* was preserved. This animal was afterwards dissected by Mr. Haines, of University College. His work was entirely independent of mine, but a comparison on my results with his brought out the fact that there was no essential difference between the Marmoset and *Midas*.

I have had the opportunity of examining two young specimens in the possession of Professor J. P. Hill, F.R.S., at University College, London. These animals were bred by Dr. Lucas at the Lister Institute. They are newly-born animals—one is a male and the other a female. I wish to thank Professor Hill for the opportunity of examining these specimens.

DISTRIBUTION.

The Hapalidæ are divided up into two genera—the true Marmosets (Genus *Hapale*) and the Tamarins (Genus *Midas*). The differences between the two genera are so few and so slight that it is doubtful if full generic rank ought to be given to the two divisions. The true Marmosets are found in the tropical forests of South America, but mainly in the Amazon Valley. One species, the Pigmy Marmoset, extends into Mexico. The Tamarins are found in the same region and also extend into Mexico.

Hapale jacchus, the Common Marmoset, according to Forbes (1896), is found only on the island of Marajo at the mouth of the Amazon. Gray (1870) considers that there are at least

four varieties of the Common Marmoset, but these forms are described as distinct species by other observers. They are:—

Hapale jacchus, the type-specimen.

Hapale albicollis (Spix), the White-necked Marmoset.

Hapale pencillata (Kuhl), the Black-eared Marmoset.

Hapale leucocephala (Kuhl), the White-headed Marmoset.

Intermediate forms are seen which combine some of the features of each of these varieties.

Hapale jacchus was first described by Linnæus (1766) under the name *Simia jacchus*. Geoffroy described three species in 1812 under the names:—

Jacchus vulgaris.

Jacchus pencillata.

Jacchus leucocephalus.

In 1820, Kuhl described the Common Marmoset under the present name—*Hapale jacchus*, while in 1823 Spix described the White-necked variety under the name *H. albicollis*.

Elliot (1912) has substituted for the generic name *Hapale* the name *Callithrix*. This change is open to grave objections, but mainly because the name had been appropriated as early as 1810 for the Tee-Tees by Geoffroy.

HABITS.

The Marmoset is a diurnal, arboreal animal living entirely in the South American tropical forest. It subsists on fruit and insects. Some observers state that it will also raid the nests of birds and devour newly-hatched chicks. Forbes says that they will eat "flesh, especially of fishes."

In captivity they are gentle, playful creatures, and if kept under warm conditions with ultra-violet light irradiation for a short time every day, they will breed (Lucas, 1927). They run about on branches of trees placed in their cages in an active manner, but are clumsy when placed on a smooth floor. The method of progression has been compared to that of a Squirrel; but this is scarcely true. When at rest they abduct the phalanges and dig the claws into the soft bark of the branch on which they perch. The hallux is maintained at right angles to the rest of the foot, but the grip it gives is very weak. The fore limbs are used for prehension of food as in other primates, but they use the manus mainly for fixing the piece of food and not for conveying it to the mouth.

Movements appear jerky, especially the movements of the head on the neck. The head can be turned through considerably more than ninety degrees, but never can it be brought round through one hundred and eighty, as *Tarsius* can do with ease (Le Gros Clark, 1924).

The fore limbs can be fully extended at the elbow. Supination and pronation can be effected readily. The hind limb is permanently flexed on the abdomen, and when at rest the thigh is close against the abdomen. The knee is always flexed. The fullest extension which I have seen did not exceed about ninety degrees.

The face does not look ventrally as in other Monkeys. It is directed forwards and ventrally; hence the angle between the line joining the snout to the occiput and the long axis of the body is considerably less than a right angle. This accounts for the tilting of the occipital squama with regard to the plane of the foramen magnum.

When feeding, the lips are not used to surround the food, but are pulled away to expose a considerable area of the alveolar region of the maxilla and mandible. The animal is able to bite sufficiently hard to perforate the skin and draw blood. The canines are usually found to have perforated deeply, while the incisors merely mark the skin.

EXTERNAL CHARACTERS.

The Hair.

The hair of the facial region is creamy over the root of the nose and the eyelids. These hairs are short and downy. Over the lower lip a number of short white hairs are to be seen. The remainder of the face is covered with blackish hair. In front, above and behind the pinna there is a marked bunch of black hair tipped with white which gives the animal a very characteristic appearance. The cranial surface of the pinna has a few sparse hairs scattered over it, but almost all are found at the helical margin. The outer surface is covered with short black hairs. The scalp is covered with brownish-black hairs which become black near their tips.

The ventral surface of the neck, thorax, and abdomen is covered with pinkish-white skin on which is distributed short brown hairs. The amount of hair seems to vary in individual animals. The perineum and the skin over the sternum are devoid of any hair. The dorsal surface of the body is covered with hair which is black for seven or eight millimetres at the root, then golden brown for the same distance, then black, and finally tipped with white.

The skin over the medial surfaces of the upper arm and thigh, the axilla, and the flexor surface of the fore arm is pink. Over these areas the black hairs are absent and short brownish hairs take their place.

The flexor surface of the tail is almost entirely devoid of hair. The dorsal and lateral surfaces are covered with black hair tipped with white. The tip of the tail has a tuft of black hair tipped with white, continuous with the other hair of the tail. There is no sign of scales on the skin of the tail.

Vibrissæ.—Vibrissæ are present. A group of three or four are seen lying on each side of the root of the nose on the supra-orbital ridge. Two or three lie in a group lateral to the anterior nares. Four large vibrissæ are found on the upper lip lying in two groups of two each near the angles of the mouth. About six vibrissæ are seen on the lower lip, but they are much shorter than the vibrissæ so far described. The latter are about a centimetre in length and are very strong. On the lower lip a number of very short stout hairs are seen which are not ordinary hairs, but are short vibrissæ. These point downwards and forwards and resemble the hairs described by Woollard as occurring in *Tursius* in the same position. (Text-fig. 1.)

Text-figure 1.



To show the arrangement of the vibrissæ on the face and the form of the external nares.

The Head.—The head is shaped like an egg. The description would be quite accurate but for an apparent flattening of the top of the skull which is caused by the upper margins of the orbit breaking the smooth contour of the cranium. The broad end of the egg forms the occiput, and the pointed end the snout. The hairy covering has been described above.

The Mouth.—The mouth is a wide slit extending as far back as the first premolar tooth on each side. The mucous margin is not everted. There are no ridges on the lip margins.

The Nose.—The anterior nasal openings are oval and are situated on the lateral surface of the snout. Their long axis lies in an antero-posterior plane. The openings face laterally and slightly forwards. Between the two nasal openings there is a well-marked depression which is caused by the cartilages surrounding the anterior nares projecting above the level of the

median plane, by the lateral position of the nasal openings and the great inter-narial distance. The nasal bones meet at an angle and form a definite ridge in the medial plane immediately above the inter-narial depression.

Ears.—Pocock (1917) has described the ears of *Hapale* in his paper on the genera of the Hapalidæ. The ears are large. The dorsal part of the pinna tends to bend at right angles to the remainder of the ear so as to lie in a transverse plane. The helix forms a broad flap with the upper and lower margins infolded as the helical margin approaches the anterior limits of the free edge of the pinna. The cartilages are described in the section on the sense organs.

Neck.—There is no well-defined neck. The angle of the mandible comes into close relation with the clavicle in the normal resting position of the head. The anterior part of the neck is sparsely covered with fine brownish hair. The hair over the posterior cervical region is intermediate in type between that on the scalp and that covering the dorsum of the trunk.

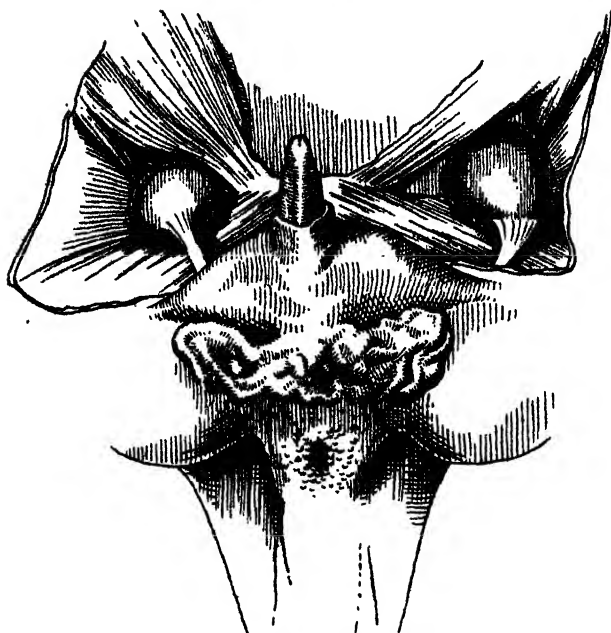
Trunk.—The thorax is heart-shaped in section. The apex of the "heart" lies on the spine. It becomes a flattened oval in the upper thoracic region, from which the shoulders spring out laterally. The scapulae are closely applied to the postero-lateral thoracic wall, and in the living animal the inter-scapular region appears as a flattened area and not sunken. The abdomen is shaped like a cone, with the base formed by the lower part of the thorax. After removal of the lower limbs this cone-shaped form is continued into the tail, which gradually narrows from base to tip.

External Genitalia.

Male (text-fig. 2).—The scrotum is a horseshoe-shaped elevation. The skin is covered with small pearly-white nodules. This nodular area of skin is continued backwards towards the anus, and surrounds that opening. The lateral masses of the genital elevation contain the testes, while the transverse ridge which joins them together across the middle line has the penis buried in it. In the middle line the tip of the penis is visible through a small circular opening. On everting the penis the glans is seen to be a cylindrical structure which has an indefinite frenum. The nipples are not present in the male. In two male specimens the testes were retracted out of the scrotum and lay obliquely in the inguinal region near the internal abdominal ring.

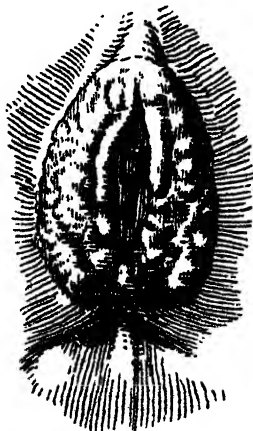
Female Genitalia.—The skin of the perineum is studded with numerous nodules closely resembling the condition seen in the male. Anteriorly they are found as far as the upper level of the body of the pubis and posteriorly as far as the root of the tail. The uro-genital cleft is separated by a considerable distance from the anus. This cleft is a slit-like recess lying between two elevations—the labia. When these are separated widely a deep pit is seen in the posterior end of the uro-genital cleft. This pit

Text-figure 2.



The external genitalia of the male. This specimen was peculiar in that the testes had been retracted upwards and lay in the inguinal fold with their upper poles in the external opening of the inguinal canal. There is no well-marked frenum. The nodular skin surrounding the anus is well marked.

Text-figure 3.



The external genitalia of the female. Note the small labia minora and the slit-like opening of the vagina.

is oval-shaped and lies about the level of the anterior edge of the inner margins of the pubic bones. It appears to be the true urogenital sinus, as into it open the urethra and the vagina. The superficial slit should then be called the vulval slit. The vagina runs backwards and upwards to the cervix of the uterus. The inner surfaces of the labia and the urogenital sinus are smooth and are covered with mucous membrane. The clitoris is completely buried, and the tips of the erectile bodies reach the surface at the most anterior edge of the vulval slit. The tips are pigmented. There is no trace of a hymen in the two female specimens examined. (Text-fig. 3.)

Two nipples are seen in the pectoral region. There are no axillary or inguinal mammary glands.

Fore Limbs.

These are relatively short and reach below the iliac crest when stretched along the lateral surface of the body. The whole limb

Text-figure 4.



The palmar surface of the hand to show the arrangement of the palmar pads. Note the small carpal pad with its group of vibrissae. See text for description.

is flattened. The outer surface is covered with the characteristic white-tipped black hair which extends as far as the wrist. The

back of the hand and the fingers are covered with fine brownish-black hair as far as the root of the claws.

Carpal Pad.—There is a carpal pad present on the ulnar side of the forearm about five or six millimetres distant from the distal end of the ulna. It is a small raised area of skin from the summit of which four small vibrissæ arise.

Palmar Pads.—There are six pads on the palmar surface of the hand. On the thenar surface there is a rectangular pad which is covered with well-marked epidermic ridges which run from the outer to the inner edge of the pad. A wide sulcus separates this pad from a well-marked pad on the hypothenar eminence. The hypothenar pad is subdivided into two—a distal triangular and a proximal trapezoid. On these pads the epidermic ridges radiate from a point near the centre of the palm to the outer edges of the pads. Four triangular pads lie at the bases of the digits; the most radial overlies the most proximal phalanx of the pollex. The next on the ulnar side of the latter overlies the same bone of the second digit. The third pad is common to the third and fourth digits, and the most ulnar of the four overlies the proximal phalanx of the little finger. Epidermic ridges are present on these, but they vary in direction. The ridges over the pollex pad are transverse from radial to ulnar edge. Those on the second pad radiate from a point on the ulnar side; hence some of the ridges are transverse and others lie in the long axis of the digit. The ridges of the third pad radiate from the palmar apex, and those on the little finger radiate from the mid-point of the ulnar edge.

Terminal pads are found on the terminal phalanx of the digits. These are flattened from side to side. The skin of the flexor surface of the first and second phalanges is bare, and is not modified to form pad-like structures. It has numerous creases. (Text-fig. 4.)

Nails.—These are claw-like structures which are flattened from side to side and have a well-marked groove on the palmar surface. The points of the claws are exceedingly sharp.

Hind Limbs.

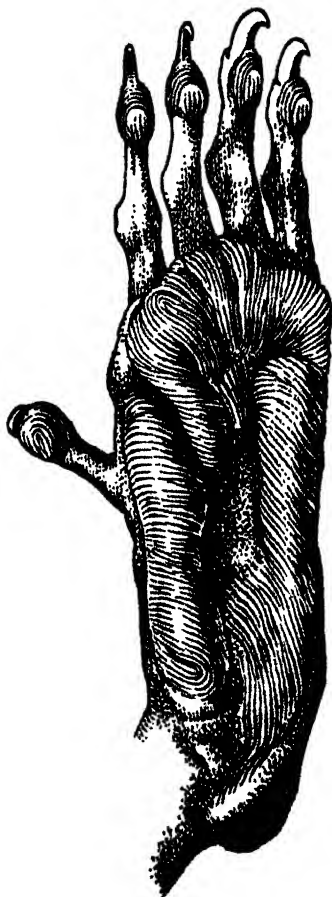
The length of the hind limbs is about equal to the crown-rump height of the animal. The muscles of the flexor and abductor regions of the thigh are very powerful, while the extensor muscles are relatively weak. The femoral and tibial lengths are about equal. The foot is elongated and relatively narrow. From the posterior margin of the os calcis to the distal ends of the plantar pads the foot is naked of hair and covered with epidermic ridges. The great length of the foot is due to the lengthening of the metatarsals and not, as in *Tarsius*, to an increase in the length of the navicular and talus.

Plantar Pads.—As in the palm, the pads can be described in three groups:—

- (a) Proximal or plantar proper.
- (b) Distal or metatarsal.
- (c) Terminal or phalangeal.

The proximal pads are two in number—one on the inner or tibial side of the foot, and one on the outer fibular side. The inner pad is a long elevation which overlies the first metatarsal and the base of the first phalanx. There is no distal hallux pad. The epidermic ridges are transverse from inner to outer edge of the pad.

Text-figure 5.



The plantar pads. Note the position of the hallux and the arrangement of the epidermic ridges.

These ridges sweep laterally over the plantar sulcus to the proximal edge of the heel. The outer pad extends from the posterior edge of the os calcis to the head of the fifth metatarsal. It is a very slight elevation above the plantar sulcus. Over the

distal end the epidermic ridges are transverse. The distal pads are three in number, although the inner one shows a sulcus which almost divides it into an inner and outer half. The outer pad overlies the base of the proximal phalanx of the fifth digit. The middle overlies the same region of the fourth, while the inner and largest is placed over the bases of the second and third digits. The subdivision of this pad would allow a separate pad for these two digits. The course of the epidermic ridges is shown in text-fig. 5.

Terminal Pads.—These have the same relations as those in the hand. The one on the pollex is very large, but is not laterally compressed as on the pollex.

Nails.—There is a flattened nail on the terminal phalanx. All the other digits bear a "side-to-side" flattened claw. On the plantar and palmar surfaces of the claws there is a distinct groove. The terminal phalanx in all the digits except the hallux is compressed from side to side and not expanded as in *Tarsius*.

Digital Formula.—The hallux is placed on the inner side of the foot about half-way along the inner edge. Consequently the first metatarsal is the smallest of the series. The third and fourth digits are equal in length and are the longest. The fifth digit is next longest and then the second. Therefore the formula is $3 \& 4 > 5 > 2 > 1$. In the hand the formula is $3 \& 4 > 2 > 5 > 1$.

Microscopic Structure of the Hair.—Mr. Martin Duncan has supplied me with the following information as to the structure of the hair of *Hapale*:—

"The hair of *H. jacchus* is of very fine texture, the diameter of the hairs ranging from 25–30 microns in diameter. The cuticular scales are well marked, imbricate, and somewhat flattened. The medulla is discontinuous, single, and flattened in the larger hairs forming the outer coat. In the fine fur the medulla is ovate in form. The medulla in these fine hairs bears a close resemblance to that of *Tarsius*. The pigment is diffuse and varies in density.

"In *Tarsius* the cuticular scales are coronal and more pointed than in *Galago*. The discontinuous medulla is relatively large, single, and ovate. The pigment is diffuse throughout the cylinder.

"In *Nyctipithecus* the cuticular scales are imbricate, crenate, and the medulla is ovate and discontinuous. The pigment of the cylinder is in the form of dense granules that are formed into chains and rods.

"The cuticular scales of *Galago maholi* are coronal in shape with simple edges. The medulla is large, discontinuous, and ovate. The pigment granules are dense and formed into chains."

The structure of the hair thus would show that *Tarsius* and *Hapale* are closely allied. *Nyctipithecus* has a more complicated arrangement of the pigment granules than *Hapale* or *Tarsius*, but the structure of the scales is not far removed from that found in either *Tarsius* or *Hapale*. (Plate II.)

THE SKELETON.

The description of the skeleton is based on a complete skeleton lent to me by Professor D. M. S. Watson and on separate bones prepared from two fresh specimens. Four complete skulls were available for description, two of which were dissected to show the relations of the parts of the orbit and the nasal cavity. One was used for a dissection of the bulla and labyrinth, while the remaining specimen formed part of a museum skeleton and was used for the general description of the skull. I had available two prepared skulls of *Midas rosalia*. These were used to compare with the *Hapale* material. I regret that I was unable to obtain a skull young enough to prepare a disarticulated specimen, and in consequence I was not able to determine the accurate detail of some of the articulations of the smaller bones. (Plate I.)

The Skull.

The *frontal bone* shows no trace of a metopic suture. Posteriorly it is prolonged into a distinct angle which separates the anterior parts of the parietals from each other. Laterally the bone articulates with the orbital plate of the malar along a line which is almost horizontal. This suture reaches the anterior edge of the orbital cavity at the junction of the superior and lateral walls. In front the bone articulates with the nasal bones and more laterally with the upper edge of the lachrymals. Within the orbit the frontal articulates with the lachrymal, the ethmoid, the palate, the lesser wing and the greater wing of the sphenoid, and finally with the malar. This articulation is along a line which is almost horizontal in its course. The bone thus forms the anterior three-fourths of the roof, the upper third of the medial wall, and practically none of the lateral wall of the orbital cavity. (See text-figs. 6, 7 & 11.) The olfactory foramen is a single opening on each side. Lying in front of the foramen and extending laterally along the superior edge of the orbit a series of small air cells are found within the bone. They extend laterally almost as far as the articulation of the bone with the malar. The bone, except in this region, is extremely thin, and there is no division of the cranial or orbital portions into inner or outer tables.

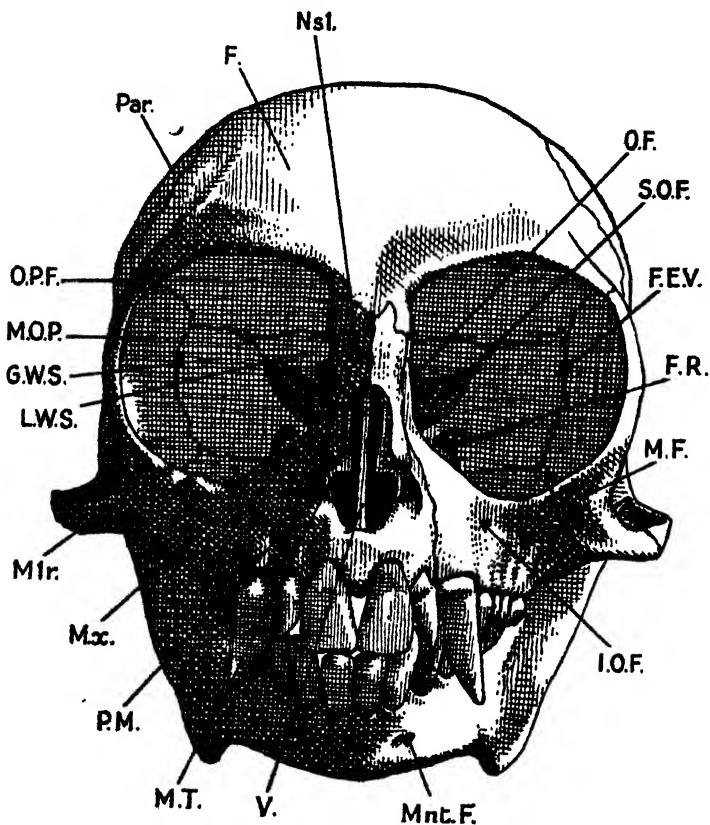
The lachrymal separates the frontal bone from the nasal process of the superior maxilla.

The Zygomatic or Malar Bone.—This bone consists of two portions—the orbital plate and the zygomatic process. The orbital portion is a thin plate of bone which forms the outer wall and most of the floor of the orbital cavity. Above, it articulates with the frontal, and inferiorly it forms the outer boundary of the slit-like inferior orbital fissure. In front of the fissure there is a short articulation with the superior maxilla. The malar foramen is complete and is not a notch as in *Tarsius*. Two small venous foramina are to be seen, one on each side of

the fronto-malar articulation. In one specimen, on one side, the malar foramen was double.

The zygomatic process of the malar extends backwards as a

Text-figure 6.



The front view of the skull.

F. Frontal bone. F.E.V. Foramen for emissary vein. F.R. Foramen rotundum. G.W.S. Great wing of sphenoid. I.O.F. Inferior orbital foramen. L.W.S. Lesser wing of sphenoid. M.F. Malar foramen. Mlr. Malar bone. Mnt.F. Mental foramen. M.O.P. Orbital plate of the malar. M.T. Middle turbinal bone. Mx. Maxilla. Nsl. Nasal bone. O.F. Optic foramen. O.P.F. Orbital plate of the frontal bone. Par. Parietal bone.

thin bar of bone which articulates along an oblique line with the zygomatic process of the temporal bone.

The Temporal Bone.—The bone forms but a small portion of the lateral wall of the cranium on the lateral surface of the skull.

In front this portion (the squamous temporal) articulates with the great wing of the sphenoid, and the line of junction of the two bones extends inferiorly, medial to the glenoid cavity and lateral to the foramen ovale, where it joins the lateral border of the bulla. Above, the squamous temporal articulates with the anterior half of the inferior border of the parietal. Above the external auditory meatus the squamous temporal ends and the mastoid portion of the bone commences. The articulation between the mastoid portion and the parietal extends posteriorly along the summit of a bony crest until the asterion is reached. Here the articulation bends down at right angles and, running forwards and inwards, terminates at the foramen lacerum posticum (jugular foramen). Along this part of the articulation the bone is in contact with the supra-occipital and the ex-occipital. From the anterior edge of the jugular foramen a suture divides the bulla from the basi-occipital and the basi-sphenoid. The anterior edge of the bulla is in contact with the posterior edge of the great wing of the sphenoid, the articulation running backwards and outwards to reach the anterior limit of the foramen ovale. At a point on the articulation between the medial border of the bulla and the basi-occipital corresponding to the mid-point of the external auditory meatus there is a small foramen. This has been described by Wortmann as transmitting a small branch of the internal carotid artery to the interior of the skull. I have not been able to demonstrate an artery passing through this foramen, but I have seen in one specimen a small vein passing through this foramen and opening into the inferior petrosal sinus. It is most unlikely that the artery described by Wortmann, in this position, really exists.

The temporal portion of the zygomatic arch forms as it passes backwards a horizontal shelf to form the glenoid surface. Immediately in front of the external auditory meatus the zygoma throws out a short post-glenoid process. Medial to the process in the angle between the bulla and the glenoid surface is the post-glenoid foramen transmitting a small vein. The anterior root of the zygoma is formed by the anterior part of the glenoid shelf. The middle root does not appear to have any connection with the posterior wall of the glenoid fossa. This wall is formed entirely by the tympanic annulus. The posterior root is continued above the external auditory meatus as a slight elevation, which is continuous with the supra-mastoid crest. Into the posterior root of the zygoma air-cells extend from the small tympanic antrum. These are described in connection with the bulla.

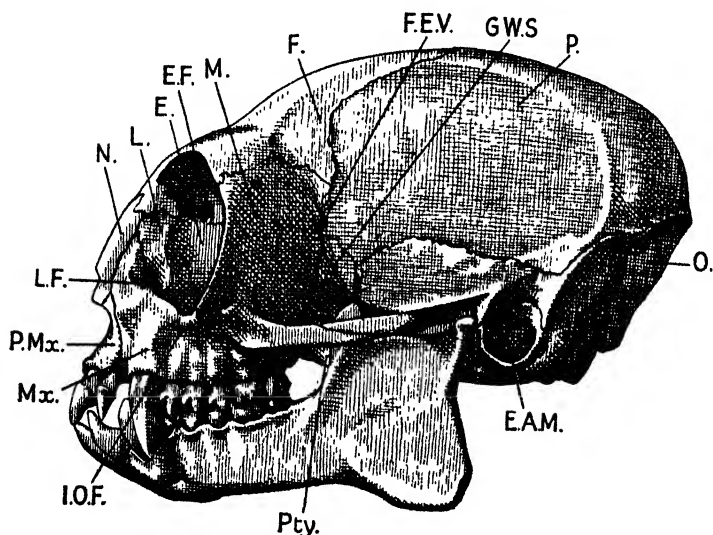
The mastoid region is only slightly inflated, but no mastoid process is developed.

In the cranial cavity the squamous temporal is shut off from the lateral wall of the cranium by the overlapping of the inferior edge of the parietal bone. It does take part in the formation of the floor of the temporal fossa (middle cranial fossa). On the cranial surface of the squamous there are several radiating furrows

which radiate from the cranial opening of the post-glenoid foramen. These lodge small veins, some of which lie below the Gasserian ganglion and are continued medially to drain the cavernous sinus. From the post-glenoid foramen there is continued backwards a small channel which becomes converted into a canal by the junction of the parietal and petrous temporal. This channel, running along the articulation, opens into the lateral sinus. It transmits a large vein.

The petrous temporal forms a triangular pyramid within the

Text-figure 7.



Lateral view of the skull.

F. Frontal bone. M. Malar bone. E. Ethmoid bone. L. Lachrymal bone. N. Nasal bone. P.Mx. Premaxilla. Mx. Maxilla. Pty. Pterygoid plate. O. Occipital bone. P. Parietal bone. G.W.S. Great wing of sphenoid. F.E.V. Foramen for emissary vein. E.F. Anterior ethmoidal foramen. L.F. Lachrymal foramen. I.O.F. Inferior orbital foramen. E.A.M. External auditory meatus.

cranium. One of the surfaces looks anteriorly and laterally, the other inwards and posteriorly. The third surface is not seen within the cranium. The anterior and posterior or postero-medial surface meet along a sharp crest which commences at the apex of the petrous and ends near the lateral wall of the skull. Along this crest is attached the tentorium cerebelli.

The bulla is described later (p. 620).

Parietal Bones.—The parietal bone articulates in front with the frontal bone, below with the lateral edge of the great wing

of the sphenoid, the squamous temporal and the posterior edge of the occipital. Medially the two parietal bones meet along the middle line. The lambdoidal suture is horizontal and runs along the summit of the nuchal line. The articulation of the great wing of the sphenoid with the parietal is about four millimetres in length and shuts off the squamous temporal from the frontal.

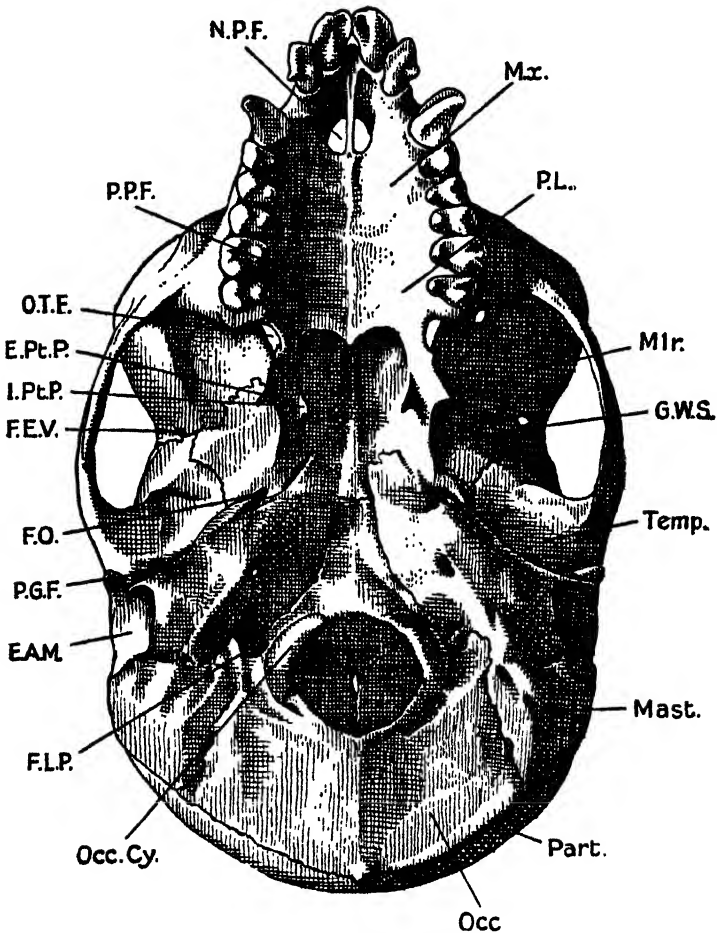
The Occipital Bone is described as consisting of four parts—the supra-, basi-, and the two ex-occipitals. The divisions between the several parts disappear at a very early age. The supra-occipital is a large fan-shaped plate of bone which articulates above with the parietals. In the middle line a small spur of bone passes upwards above the nuchal line and between the two parietals for a short distance. From this spur to the posterior border of the foramen magnum there is a well-marked median ridge (much more accentuated in *Midas*). The nuchal line extends laterally from the lambda along the lambdoidal suture to the asterion, where it is continuous with the mastoid portion of the line and is continued through this ridge or crest to the posterior or supra-mental root of the zygoma. Below the nuchal line there are well-marked muscular impressions. The area for the complexus is very large and approaches closely the foramen magnum. The area for the superior oblique is only slightly smaller than the area for the complexus. On the inner surface of the supra-occipital three shallow depressions are seen for the lodgement of the cerebellum. On the lateral edge of the bone are seen two well-marked grooves which pass downward and forwards to the jugular foramina. The foramen magnum lies well behind the junction of the anterior two-thirds with the posterior third of the skull. It is almost circular, being but a millimetre (or two, in one specimen) more in the transverse than in the antero-posterior diameter. With the skull fixed in the Frankfurt plane, the plane of the foramen magnum faces downwards and backwards, making an angle of about 30 degrees with the Frankfurt plane. The condyles lie mainly in front of the greatest transverse diameter. Their convex surfaces are divided into two parts—an anterior two-thirds, which faces outwards and downwards, and a posterior third, which faces almost directly backwards. The anterior edges of the condyles are separated by a distance equal to half the transverse diameter of the foramen.

The basi-occiput is prolonged forward between the two bullæ, becoming gradually narrower until it meets with the basi-sphenoid. Sometimes a small foramen is seen between the two bones. This is the cranio-pharyngeal canal.

The condyloid foramen is almost hidden by the large condyles. It is always single. The jugular foramen consists of two parts—the anterior, which is often single but may be subdivided into three foramina (an anterior, which transmits the inferior petrosal sinus, and a medial and lateral for the passage of the IXth, Xth, and XIth cranial nerves), and the posterior compartment for the transmission of the lateral sinus.

The *Sphenoid bone* consists of a body, a great and a lesser wing, and the pterygoid laminae. The body in young specimens consists of two parts—the pre- and the post-sphenoid separated by a

Text-figure 8.



The ventral view of the skull.

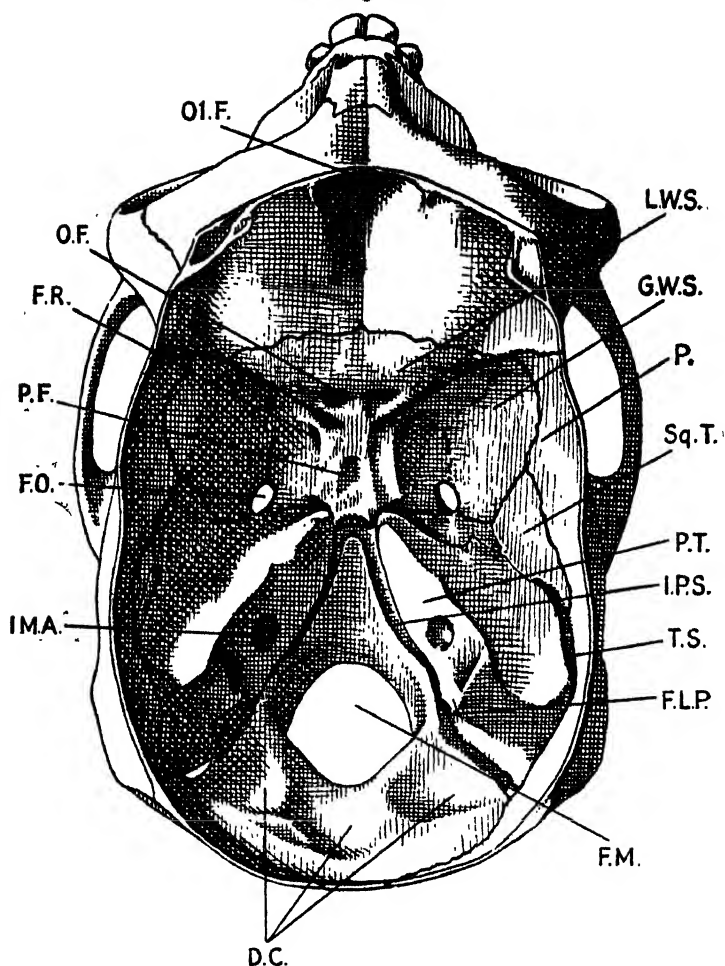
E.A.M. External auditory meatus. E.Pt.P. External pterygoid plate. F.E.V. Foramen for emissary vein. F.L.P. Foramen lacerum posticum. F.O. Foramen ovale. G.W.S. Great wing of sphenoid. I.Pt.P. Internal pterygoid plate. Mast. Mastoid region of the temporal bone. Mir. Malar bone. Mx. Maxilla. N.P.F. Naso-palatine foramen. O.T.F. Orbito-temporal foramen. Occ. Occipital bone. Occ.Cy. Occipital condyle. P.L. Palate bone. P.P.F. Posterior palatine foramen. Part. Parietal bone. P.G.F. Post-glenoid foramen. Temp. Temporal bone.

thin plate of cartilage. The shape of the body in the adult is a thin rod which carries on its lateral aspects the two wings. The pre-sphenoid and the lesser wings are fused together at an early age. In front this composite bone articulates with the frontal within the orbital cavity. From the median plane of the bone a thin septum passes downwards—the septum of the pre-sphenoid described by Woollard in *Tarsius*. This plate of bone forms a considerable portion of the medial wall of the orbital cavity, hence the two cavities in this region are separated from each other by this thin plate, a condition which is identical with that in *Tarsius*. The septum is overlapped laterally for a short distance by the orbital plate, which shuts part of the septum from the medial walls of the orbit. Below, it articulates with the vomer. The ethmoidal septum lies in front of the sphenoid and forms the upper half of the nasal septum in the anterior part of the nasal cavity. The root of the lesser wing is perforated by the optic foramen, which is separated from the superior orbital fissure by a thin bony bar. The lateral extremity of the lesser wing is shut off from contact with the antero-inferior angle of the parietal bone by a small spur of bone from the frontal. This spur is perforated by a foramen which is often double. The foramen transmits meningeal vessels from the orbital cavity which ramify over the lateral surface of the cranial cavity. Along its posterior border the lesser wing articulates with the great wing from the superior orbital fissure to the lateral extremity of the small wing.

The great wing forms the floor of the temporal fossa of the cranial cavity and the posterior third of the lateral wall of the orbit. Anteriorly it is in contact with the malar for a short distance as far as the upper edge of the inferior orbital fissure. Posteriorly the wing articulates with the squamous temporal as far as the lateral margin of the foramen ovale. The wing from the foramen ovale to the middle line is deeply notched for the reception of the apex of the petrous temporal, which is carried forward to terminate in a serrated edge near the body of the sphenoid. The exact pattern is seen in text-figure 8. The great wing takes part in the formation of two foramina—the foramen ovale and the superior orbital fissure, which are formed at the articulation of the wing with the petrous temporal and the lesser wing respectively. The wing is perforated by the foramen rotundum below the superior orbital fissure. A deep groove lies on the lateral side of the body at the junction of this with the great wing. Anteriorly the groove terminates at the foramen rotundum, and apparently the groove lodges the maxillary division of the trigeminal nerve. The foramen ovale described above transmits the middle meningeal artery and the third division of the trigeminal nerve. Hence the foramen is properly the foramen ovale cum spinosum. The meningeal artery is very small.

The body of the sphenoid is narrow and shows a shallow

Text-figure 9.



Internal view of the base of the skull.

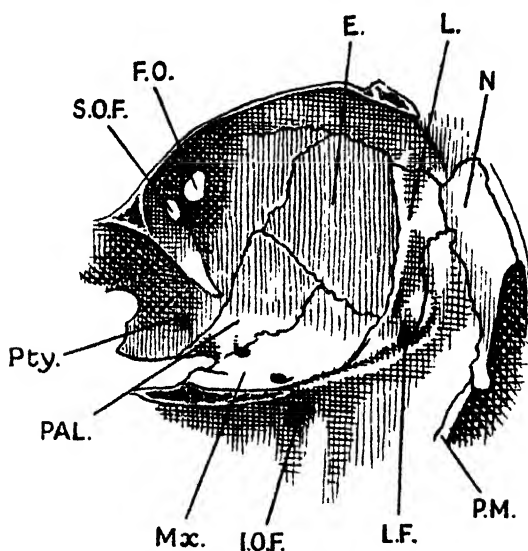
Ol.F. Olfactory foramen. O.F. Optic foramen. F.R. Foramen rotundum. P.F. Pituitary fossa. F.O. Foramen ovale. IMA. Internal auditory meatus. D.C. Depressions on occipital bone for cerebellum. F.M. Foramen magnum. F.L.P. Foramen lacerum posticum. T.S. Transverse sinus. I.P.S. Inferior petrosal sinus. P.T. Petrous temporal. Sq.T. Squamous temporal. P. Parietal. G.W.S. Great wing of sphenoid. L.W.S. Lesser wing of sphenoid.

depression for the reception of the pituitary gland. The body is made up of a mass of fine cancellous bone covered with a thin layer of compact tissue. There is no sphenoidal sinus.

The pterygoid laminae spring from the inferior surface of the great wing. The lateral lamina is large and closely applied to its medial surface is the medial plate, which is very small. The pterygoid fossa is very shallow. Posteriorly the lateral lamina terminates well in front of the foramen ovale. In front it articulates with the palate bone. The line of articulation is vertical and appears to terminate in the region of the orbital opening of the foramen rotundum.

The *Ethmoid bone* consists of a medial plate and two lateral plates. The medial plate forms part of the septum of the nose.

Text-figure 10.



The medial wall of the orbit.

L. Lachrymal. N. Nasal. P.M. Pre-maxilla. L.F. Lachrymal foramen. I.O.F. Infra-orbital foramen. Mx. Maxilla. Pal. Palate. Pty. Pterygoid. F.O. Foramen opticum. S.O.F. Superior orbital fissure. E. Ethmoid.

At its upper border it joins the lateral laminae, but no cribriform plate is formed, nor are any cells developed in the bone. The olfactory foramen is a single opening which is directed anteriorly and downwards. The lateral laminae form part of the medial walls of the orbits and articulate in front with the lachrymal and posteriorly with the orbital plate of the palate. The orbital or lateral plate of the ethmoid also forms part of the lateral wall of the nasal cavity. The relations of the bone are clearly seen in text-figures 10, 11 & 12.

Palate Bone.—This bone consists of two parts—a vertical and

a horizontal plate. The vertical plate lies almost entirely within the orbital cavity. There it is in contact with the septum of the pre-sphenoid and so forms part of the medial wall of the orbit. It passes downwards and laterally, and forms the medial boundary of the inferior orbital fissure. Below the fissure the bone is carried downwards a short distance into the pterygoid fossa and forms the medial wall of this space, with the lateral pterygoid plate of the sphenoid. The two orbital plates of the palate approach each other above and are only separated by the thin septum of the pre-sphenoid. From its inferior part the horizontal plate of the palate springs out to form the posterior third of the hard palate. The two horizontal plates articulate and are prolonged posteriorly into a well-marked posterior palatal spine. The articulations have been mentioned already in the descriptions of the other cranial bones.

The *Superior Maxilla* forms the medial two-thirds of the inferior border of the orbit and the inferior half of the medial border. Laterally it articulates with the malar, medially with the pre-maxilla, nasal, and lachrymal. Superior to the frontal process of the maxilla the nasal and lachrymal articulate, so shutting off the frontal from articulation with the maxilla and allowing the lachrymal to take part in the formation of the medial border of the orbit. The maxillary nerve is contained within a bony canal which commences at the anterior boundary of the inferior orbital fissure and emerges on the face at the infra-orbital foramen. The infra-orbital foramen may be double. It is not uncommon to find that the inferior orbital fissure is divided into two parts by a bony bridge formed by the articulation of the malar and the superior maxilla. The anterior part is small and opens directly backwards into the temporal fossa.

The maxillary antrum is small and does not extend more laterally than the medial edge of the canine tooth. The roots of the premolars and the molars lie in relation to the floor of the orbital cavity.

The *Pre-maxilla* is small. It bears the four incisor teeth of the upper jaw. The two halves are fused in the middle line. The bone is prolonged upwards into two thin processes which articulate above with the nasals and posteriorly with the maxillæ. The pre-maxilla thus forms the whole of the floor and the lower half of the lateral wall of the bony anterior nares. The articulation between the pre-maxilla and the maxilla is continued on the hard palate from the diastema between the lateral incisor and the canine to the anterior palatine foramina, which are very large.

Nasal Bones are small flat plates of bone which articulate with each other for more than half their length in the median plane. Above they are in contact with the frontal, and posteriorly with the lachrymal and the superior maxilla.

Lachrymal bone.—This is a small quadrangular bone lying on the medial wall of the orbit and extending downwards on to the

floor internal to the inferior orbital edge. The bone is almost entirely within the orbit, only a small portion emerging on the face to articulate with the nasal bone. The opening of the lachrymal duct is well within the margin of the orbit.

Vomer.—The vomer is a thin lamina which forms the posterior part of the bony nasal septum. Above it articulates with the ethmoid and the pre-sphenoid, and below with the palatal crest along the upper surface of the hard palate. In front it joins the septal cartilage. Its relations are seen in text-figure 12.

Nasal Turbinate Bones.—These are described in detail in the description of the nasal cavity.

The Orbital Cavity.

The orbital cavity is shaped like a cone with the base at the anterior opening and the apex at the optic foramen. The anterior opening is slightly flattened along the mesial portion, and the edges of the opening, with the exception of the mesial, are slightly inflected. Laterally the malar bones are bowed out to form the major part of the lateral wall. This wall curves gradually medially to pass into the floor of the cavity. The malar ends at the lateral edge of the inferior orbital fissure, and in front it articulates with the superior maxilla. The inferior orbital fissure is covered by a thin membrane which is continuous with the periosteum of the bones forming the boundaries of the opening. The medial wall and the medial part of the floor are formed by the following bones: the superior maxilla, the lachrymal, the ethmoid-lateral plate, the septum of the pre-sphenoid, the palate, and the main mass of the pre-sphenoid. The posterior third of the lateral wall is formed by the great wing of the sphenoid. The apex of the cavity is formed by the lesser wing, which is perforated by the optic foramen.

The optic foramen is oval with its long axis directed downwards and medially. It is the largest foramen leading from the cranial cavity with the single exception of the superior orbital fissure. The superior orbital fissure is drop-shaped, with the point directed above and externally. Its upper boundary consists of the lesser wing of the sphenoid, and the lower boundary is formed by the great wing.

Lying below the superior orbital fissure is a small circular opening—the foramen rotundum. This foramen lies outside the orbital cavity in the recent state, as the membrane which closes over the inferior orbital fissure is continued backwards as far as the inferior edge of the superior orbital fissure.

The inferior orbital fissure is a narrow slit-like cleft running from the postero-medial angle of the cavity towards the antero-lateral. From the anterior end of the fissure the infra-orbital canal commences, and, running straight forwards, it opens on the face at the infra-orbital foramen.

The lachrymal canal passes downwards between the lachrymal and the frontal process of the superior maxilla and opens into the

nasal cavity below the inferior turbinate bone. The ethmoidal foramen is situated at the articulation of the frontal and the lateral plate of the ethmoid. It is directed upwards and medially. It transmits an artery from the ophthalmic artery, which supplies the nasal mucous membrane of the lateral wall in its upper half and a small area of the nasal septum. On the lateral wall, where the tip of the great wing of the sphenoid articulates with the frontal, is a foramen which transmits an artery and vein. These are meningeal arteries and supply the meninges over the antero-lateral part of the cranial wall (Mensa). On the lateral wall the small zygomatic foramen opens lateral to the anterior end of the inferior orbital fissure.

The floor of the cavity is in part formed by the superior maxilla, which is not expanded much in depth, hence the roots of the premolars and molars lie close to the floor of the orbit. The maxillary antrum is very small and lies entirely in the lateral wall of the nose and hardly penetrates laterally.

Nasal Cavity.

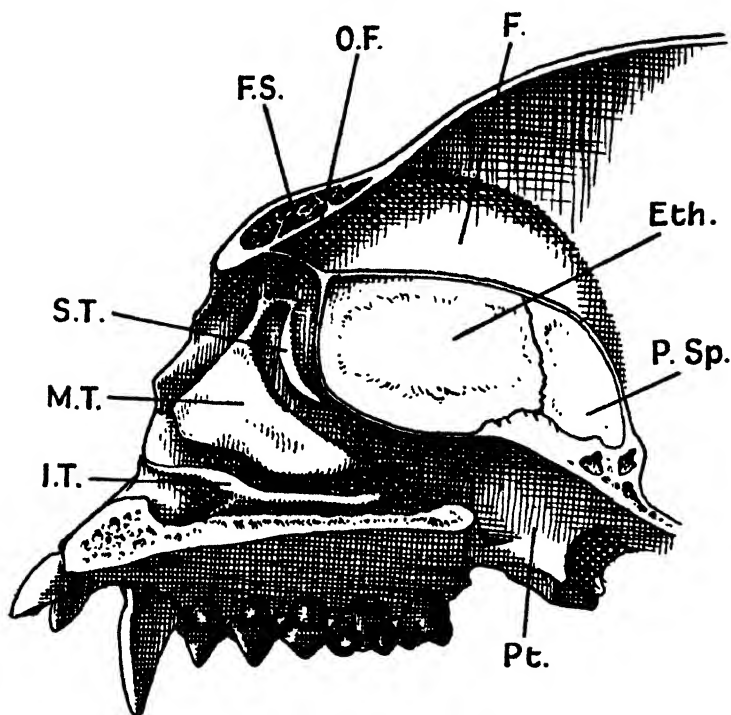
The nasal cavity lies well in front of the anterior limit of the cranial cavity. A line passing vertically downwards from the posterior edge of the olfactory foramen divides the nasal cavity into two parts—an anterior five-sixths and a posterior sixth. The posterior portion is a tubular connection between the main nasal cavity and the pharynx. Hence, in this respect there is a condition which is exceedingly primitive, and Fischer's remarks on the cranium of *Tarsius*, which presents a similar arrangement, may be applied to *Hapale*—that the condition closely resembles the reptilian arrangement. His conclusion that this pushing forwards of the nasal region is due to the enlargement of the orbits is probably true, for, although in *Hapale* the orbits are not enlarged to the degree seen in *Tarsius*, yet the medial walls of the cavities for the eyes are for a considerable extent composed only of the pre-sphenoid septum—a condition identical with that of *Tarsius*.

The main part of the nasal cavity is very narrow from side to side, and the lateral and medial walls lie almost parallel to each other. Into the cavity project three turbinate bones—superior, middle, and inferior. The superior turbinate is a thin crescentic plate of bone. It commences immediately posterior to the olfactory foramen and passes downwards and backwards to the junction of the tubular posterior nares with the nasal cavity. It is covered with olfactory epithelium. The middle turbinate bone is a thin triangular plate attached to the lateral wall immediately in front of the superior turbinate. It has an upper angle which lies immediately below the olfactory foramen, a posterior angle which extends for a short distance into the tubular nares, and an anterior angle which is free and projects forwards towards the anterior nares. The inferior turbinal consists of a thin plate of bone attached to the lateral wall along the antero-posterior

axis of the cavity. It extends forwards a little beyond the anterior limit of the middle turbinal, and backwards as far as the posterior angle of the middle turbinate bone.

The lateral wall is composed of the superior maxilla, the ethmoid, and the palate bones; the roof of the nasal bones and the medial plate of the ethmoid. In addition to these bony structures the lateral wall is formed anteriorly by the alar cartilages, which are attached behind to the nasal bones.

Text-figure 11.



The lateral wall of the nasal cavity.

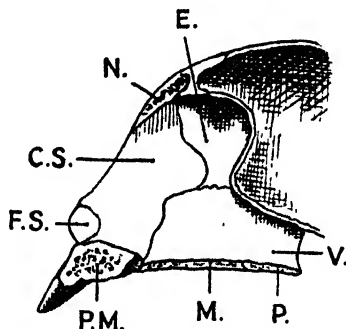
Eth. Ethmoid. F. Frontal. F.S. Frontal sinus. I.T. Inferior turbinal. M.T. Middle turbinal. P.Sp. Presphenoid. Pt. Pterygoid. O.F. Olfactory foramen. S.T. Superior turbinal.

The septum is shown in text-figure 12, and from this the relations and the arrangement of the various structures can be seen. The alar cartilages bend inwards and at first have a considerable interval between them which is occupied by fibrous tissue. As the cartilages are traced backwards the medial parts of the cartilages approach together and eventually fuse in the middle line to

form the perpendicular or septal cartilage. Behind, this cartilage is attached to the ethmoidal part of the septum and to the anterior edge of the vomer, and above to the articulation of the nasal bones. The bony septum is continued backwards as far as the posterior palatal spine. Posterior to the anterior palatine foramina lie the organs of Jacobson. In their arrangement they closely resemble those of *Tarsius*. The naso-palatine ducts are very minute. No mouth opening can be determined in any of the specimens examined in a fresh state. The ducts incline upwards and backwards to reach the nasal cavity in the region of the anterior end of the vomer, where it articulates with the crest along the superior maxilla.

Woollard, in his description of the nasal cavity of *Tarsius* (p. 1084), points out the peculiar arrangement of the ethmoid

Text-figure 12.



The medial wall of the nose. Semi-diagrammatic.

P. Palate, horizontal plate. V. Vomer. E. Ethmoid. N. Nasal bone, cut. C.S. Cartilaginous septum. F.S. Fibrous septum. P.M. Premaxilla. M. Maxilla.

and the part it plays in the formation of the nasal cavity. It is of interest to compare the ethmoid of *Hapale* with that of *Tarsius*, for the structure appears to be identical. The bone consists of three perpendicular plates of bone lying almost parallel to each other. Above, they are fused together posterior to the olfactory foramen, and for a short distance there appears a small central mass within the anterior fossa of the cranial cavity. Woollard mentions that in *Tarsius* this does not take place. The medial plate is articulated to the anterior edge of the pre-sphenoid and lies in a groove formed by two small ridges along the anterior edge of the sphenoid. This plate is quadrangular and very thin. The lateral plates are also quadrangular, but are not drawn out as in *Tarsius*. They are more compressed antero-posteriorly. They overlap the septum of the pre-sphenoid for a short distance

on the medial wall of the orbit. In front they articulate with the lachrymal, and above with the frontal. Posteriorly the plate meets the palate, and below it lies in contact with the superior maxilla.

The tubular choanæ commence immediately below the antero-inferior angle of the pre-sphenoid and are much shorter than in *Tarsius*. The lateral wall is made up by the medial pterygoid plate, the palate, and the lateral plate of the ethmoid. The palate is continued upwards lateral to the tubular choanæ, and lies lateral to and overlapping for a short distance the sphenoidal septum.

It is impossible to regard the arrangement of the nasal cavity as anything else than a close approximation to the *Tarsius* condition. There have been minor changes, but these are easily explained by the great differences in the size of the eyes and the enlargement of the orbits noted in *Tarsius*. This supports the view that in *Hapale* the nasal organs are reduced a stage further than in *Tarsius* and that the changes in the region are closely associated with a retraction of the muzzle.

Cranial Foramina.

The olfactory foramen is single. There is no cribriform plate of the ethmoid. The foramen faces downwards and forwards. The crista galli is very thin but well marked.

The optic foramen has been described above.

The superior orbital foramen transmits the third, fourth, sixth, and the ophthalmic division of the fifth nerve. There is no separate foramen for the third nerve as in *Tarsius*.

The foramen rotundum is situated below the superior orbital fissure foramen. It is almost circular. There is a short canal for the transmission of the maxillary division of the fifth nerve.

The foramen ovale is almost as large as the optic foramen, and in some specimens it is slightly larger. It transmits the small middle meningeal artery and the third or mandibular division of the fifth nerve. It is really the foramen ovale cum spinosum.

The internal auditory meatus is large and transmits the seventh and eighth nerves and the internal auditory artery. It lies medial and inferior to the fossa for the parafoveolus.

The jugular foramen transmits the ninth, tenth, and eleventh nerves as well as the inferior petrosal sinus and the lateral sinus.

The condylar foramen is usually single. The hypoglossal nerve may pass through it in two or three filia which perforate the dura mater separately. Fieandt has investigated the method of formation of the hypoglossal nerve in most mammals including *Hapale*.

The post-condyloid foramen is absent.

Venous sinuses.

The superior longitudinal sinus terminates in the region of the lambda by dividing equally into two small channels which pass

laterally along the lambdoidal suture to reach the posterior part of the petrous temporal, where they terminate by entering into the large lateral sinus. There is a small occipital sinus which commences in the region of the foramen magnum and enters the superior longitudinal sinus at its bifurcation.

The lateral sinus is formed by the junction of the lateral branch of the superior longitudinal sinus with a large sinus, which arches over the lateral extremity of the petrous temporal and is partly embedded in the articulation of that bone with the parietal. This supra-petrous sinus terminates at the cranial opening of the post-glenoid foramen. A large vein passes out through this foramen and forms the external jugular vein. Into the anterior extremity of the supra-petrous sinus several small veins terminate. These drain the floor of the temporal fossa. One of the veins passes posterior to the foramen ovale and joins the cavernous sinus, but this connection is very small.

The cavernous sinus occupies its usual position and is drained posteriorly into the inferior petrosal sinus, which passes out through the jugular foramen as a separate vein joining the internal jugular vein immediately outside the skull.

The anterior cranial fossa and the lateral cranial wall are drained by a system of small veins which converge on the foramen at the tip of the great wing of the sphenoid where the latter articulates with the frontal bone. A large vein is formed which drains into the orbital cavity. A connection is found between the anterior system and the system of veins draining into the post-glenoid foramen.

The whole arrangement appears to be a very primitive one and is associated with the fact that there is a very minute middle meningeal artery. I do not propose to give these veins any definite names as I have not yet found complete references to the condition in other animals. The general arrangement is similar to that in *Ptilocercus* described by Le Gros Clark (1926).

On the anterior aspect of the petrous temporal medial to the post-glenoid foramen a small vein emerges which runs medially to join the cavernous sinus. This may be the meningeal vein which accompanies the stapedia artery. On the other hand, it may be that it is a very minute stapedia artery, although on dissecting the carotid canal very carefully in the specimen in which it was seen—a dried skull—there was no trace of a foramen on the wall of the carotid canal through which a stapedia artery may have passed.

The Auditory Bulla.

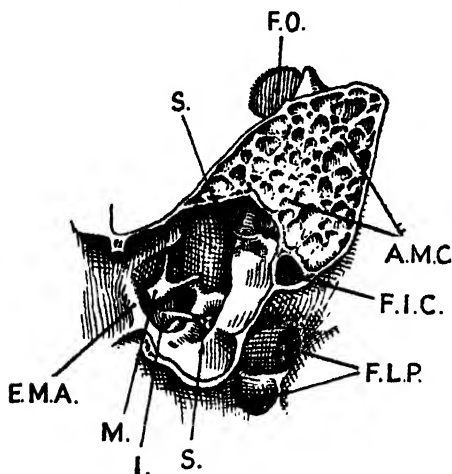
The bulla is a conical structure with its apex lying near the apex of the petrous temporal and with a rounded base which is situated more laterally than the apex. The long axis is therefore at a slight angle to the basi-cranial axis. The angle between the long axes of the bullæ is about 45 degrees (text-fig. 9). It is divided by a shallow groove on the inferior surface into an

anterior and a posterior part. This groove runs laterally from the foramen for the internal carotid artery and inclines forwards. The groove is better marked in *Midas* than in *Hapale*. On the lateral side lies the external auditory meatus. The lateral boundary runs from the anterior edge of the external auditory meatus to a short distance posterior to the foramen ovale. In this part of its course the bulla lies close to the great wing of the sphenoid. It is marked off by a suture from the zygomatic part of the temporal bone. This suture lies posterior to the post-glenoid foramen. On the apex is the opening for the auditory tube and the tensor tympani muscle. This opening lies posterior and slightly medial to the foramen ovale. The bulla is prolonged forwards medial to the foramen ovale into the tip of the petrous temporal, so forming a distinct notch between the great wing of the sphenoid and the basi-sphenoid. The apex does not reach forward to the pterygoid plate. The medial border lies adjacent to the basi-sphenoid and the basi-occipital. At the posterior end of the border lies the foramen lacerum posticum, which is bounded laterally by the bulla and medially by the ex-occipital. The posterior edge or base fades gradually into the mastoid portion of the temporal. At the lateral part of the base close to the posterior limit of the external auditory meatus lies the sterno-mastoid foramen. The foramen lacerum medius is absent. The external auditory meatus is large and the tympanic ring is expanded and fused with the bulla, making it impossible to determine the actual limits of the two parts. There is no mastoid process, but the area mastoidea is large.

Van Campen has described the internal structure of the bulla in *Midas rosalia*, the closely-allied species to *Hapale*. There are no differences between his description and my findings. When the inferior wall of the bulla is removed, the bulla is seen to consist of an antero-medial and a postero-lateral division divided off from each other along the line of the groove described on the inferior surface. The antero-medial is shut off from the postero-lateral compartment by an almost complete bony septum. The antero-medial division consists of a mass of small air-cells—the cellulæ petrosæ. The postero-lateral compartment is the middle ear or the tympanic cavity. The tympanic cavity may be described as a room three times as long as it is broad and with a height equal to twice the width. The anterior end is funnel-shaped, and leads up into a rounded canal which has on its medial wall a small ridge which partially divides the canal into an upper portion for the tensor tympani muscle and a lower for the auditory tube. The ridge is carried to the lateral wall by a fibrous sheet in the recent state, so dividing off the tube from the muscle. The medial wall has a small foramen lying medial to the opening of the auditory tube. This opening leads into the petrous air-cells and the medial wall of the anterior third of the tympanic cavity. The middle third of the cavity is more complex. On the medial wall a rounded projection is seen divided

into an anterior and a posterior part by a shallow groove. This is the promontory. The posterior part is formed by the first turn of the cochlea, and the anterior is caused by the more apical turns. There are probably three or two and a half turns in the cochlea. It was not found possible to determine this accurately without section of the bone. The lateral wall is defective, being covered by the tympanic membrane. The roof of this part of the cavity has a small almost circular opening leading into the epitympanic recess in which are lodged the heads of the malleus and the incus.

Text-figure 13



The auditory bulla dissected. The ventral wall has been removed. The bulla is seen to be divided into two parts by a bony septum. The postero-lateral compartment is large, but the anterior one is broken up into small cells by thin bony septa.

F.O. Foramen ovale. A.M.C. Antero-medial compartment consisting of small air-cells. F.I.C. Foramen for internal carotid artery. F.L.P. Foramen lacerum post. subdivided into two by a thin plate of bone. M. Malleus. I. Incus. S. Stapes. E.M.A. External auditory meatus. S. Septum.

The long process of the malleus projects downwards and medial, and posterior to it is the stapedia process of the incus. On the medial wall lying above the bony projection caused by the first turn of the cochlea is an ovoid opening. The opening leads into a tubular canal, to the bottom of which the foot-piece of the stapes is attached to the membrane covering the fenestra ovalis. There is no bony canal between the two legs of the stapes. Inferior to the canal leading to the fenestra ovale and slightly posterior lies the fenestra rotunda. Strictly speaking, the fenestra rotunda lies in the posterior third of the tympanic cavity. This

part of the cavity lies entirely posterior to the posterior margin of the external auditory meatus. On the posterior wall is a small foramen which communicates with the air-cells of the mastoid region. This foramen is not always present.

The epitympanic recess is a very small cavity. Posteriorly and superiorly it has a relatively large foramen which pierces the tegmen tympani and opens into a small space which appears to be homologous with the antrum mastoidea. From this cavity a number of air-cells open out into the squamosal and the mastoid region. These air-cells are quite distinct from the air-cells in the anterior part of the petrous temporal.

The petrous cells which communicate with the tympanic cavity through the small foramen near the canal for the auditory tube penetrate anteriorly into the most anterior part of the petrous temporal and into the tegmen. Hence they form part of the cranial wall. The cells are continued posteriorly as far as the canal for the internal carotid artery, and thus lie on the medial side of the middle part of the tympanic cavity.

The air-cells in the mastoid region are separate from those in the squamosal. The squamosal cells, which are few in number, open separately into the small tympanic antrum near the foramen pneumaticum, which connects the whole of the posterior group of air-cells with the tympanic cavity. The mastoid cells penetrate from the region of the antrum lateral to the horizontal semi-circular canal to reach the mastoid area.

The Course of the Internal Carotid Artery.

The internal carotid artery enters the petrous temporal through a large foramen situated on the medial wall of the bulla. This foramen lies on the transverse plane connecting the mid-points of the two bony external auditory meatuses. It lies anterior to the posterior lacerated foramen. The foramen corresponds to the most posterior limit of the petrous air-cells, and is therefore at the posterior edge of the septum separating these cells from the tympanic cavity. It is also immediately anterior to the most anterior part of the labyrinth in this region, which is the first turn of the cochlea. Passing upwards, the artery lies in a canal situated in the bony septum described above, and then turns forward at the level of the foramen connecting the petrous air-cells with the tympanic cavity. The artery emerges at the apex of the petrous temporal near the posterior clinoid process. The whole course is in a vertical plane which is inclined to the median plane of the skull at an angle of about thirty degrees. There is no stapedia artery.

Formation of the Bulla.—I have not been able to secure a specimen young enough to show the exact limits of the tympanic and the petrous parts of the temporal bone in the formation of the bulla. Van Campen suggests that the whole of the lateral wall is formed by the expanded tympanic, and that also in the region of the external meatus the tympanic expands inwards to

form a considerable part of the floor of the middle part of the tympanic cavity.

Facial Canal.—The facial nerve is enclosed in a complete bony canal. The canal passes laterally for a short distance from its commencement within the deep fossa of the internal auditory meatus. It then makes a right-angle bend in the same horizontal plane, and passes directly backwards over the fossa for the para-flocculus of the cerebellum. It then passes downwards in a vertical direction to reach the sterno-mastoid foramen. The stylo-mastoid foramen is situated posterior to the external auditory meatus and a short distance medial to this opening. The foramen marks the most posterior limit of the tympanic cavity and the most anterior part of the mastoid air-cells.

Auditory Ossicles.

The work of Doran on the auditory ossicles (1871) included an account of those of *Hapale*. He mentions that he found several small differences in the form of the ossicles in different species of *Hapale*. I have examined the ossicles in seven species of *Hapale* and in ten individuals of *Hapale jacchus*. The differences he notes as taking place in different species are to be seen within the confines of a single species. His summary contains all the information which is of importance in this study.

"The malleus of *Hapale* is intermediate between that found in the Cebidæ and the Nycticeboid Lemurs. The articular surface is always narrower and deeper in *Hapale*, and the whole body is bent more inwards on the manubrium. The head is no longer vertically than in *Nycticebus*. The body of the incus is square in *Hapale jacchus*, but in *H. melanura* it is high and narrow as in *Nyctipithecus*.

"The stapes has a long head, or rather the crura are fused half way to their insertion, where they suddenly diverge towards the base. In this respect they are very like the marsupial condition, where the crura are not fused throughout. Hence in *Hapale* there is found the lowest type of ossicle in all the Primates.

"There is no neck to the malleus, but this is due to the bending down below the articular surface of the head, which actually lies in the axis of the manubrium."

The Mandible.

The two halves of the mandible are fused at the symphysis. The horizontal ramus is relatively deep. It makes an angle with its fellow of the opposite side of about 45 degrees. The mental foramen lies opposite the root of the first premolar tooth. Posteriorly the mandible is produced out into a rounded angle. In *Midas* the angle is produced into a point near the upper limit of the angular region. The two angles are inflected slightly, and are also carried inwards for a short distance to produce a fossa for the insertion of the pterygoideus internus muscle. The horizontal ramus meets the ascending ramus to form an obtuse

angle. Hence the anterior edge of the ascending ramus passes slightly backwards. The coronoid process is directed posteriorly and upwards, and is separated by a wide, shallow groove or notch from the condyloid process. In *Midas* the coronoid process is deeper and less wide. The condyloid process forms a convex oval-shaped surface whose long axis is directed slightly posterior and medially. The axes of the condyles make an angle of about 120 degrees with each other.

The opening of the inferior dental canal is on a level with the upper level of the alveolar margin and directly under the middle of the notch of the ascending ramus. In *Hapale* the lingula is absent, but in *Midas* a well-marked process is seen.

Teeth.

The dental formula of all the Hapalidæ is

$$\begin{array}{cccc} 2 & 1 & 3 & 2 \\ \hline 2 & 1 & 3 & 2 \end{array}$$

On the reduction of the molars from three to two, Bolk has brought forward a theory to derive the Old World forms from an ancestor akin to the Hapalidæ. The theory has been discounted on embryological and other grounds, and is not accepted. The significance of the absence of the last molar has been variously interpreted, but there seems to be little doubt that *Hapale* has carried the reduction of the third molar to a stage further than is seen in other living Primates. Gregory regards the atrophic nature of the third molar as a primitive Primate characteristic, and has noted that in some of the fossil forms from the Eocene this condition of molar reduction is suggested.

The teeth of this animal have been described in many books, and it would be superfluous to add yet another description to the literature. It will be enough to quote the words of Gregory (1922) in his book on the evolution of the human dentition (p. 228 and p. 230):—

“The molar series, both upper and lower, are more or less retrogressive in size and probably also in the form of the crown. Starting with *Nyctipithecus*, of the Cebidæ, and passing to the Tamarin (*Seniocabus*) and the other genera of the Hapalidæ, we may observe traces of this retrogressive process. In *Nyctipithecus* the first upper molar, which in most mammals is conservative in form, retains the subquadrate contour which is characteristic of this tooth in the other Cebidæ; but the second upper molar is reduced in size and subtriangular in form, through the partial suppression of the postero-internal corner. The third upper molar (in *Nyctipithecus*) is very retrogressive, only the anterior moiety remaining, the posterior moiety being barely if at all represented. The Hapalidæ have carried this process much further, suppressing the third molars entirely and often reducing the second molars to a form quite like that of the third molars of *Nyctipithecus*. Even the first molars of the Hapalidæ apparently

have shared in this general retrogressive evolution, for in *Midas* the metacones of the first molars are reduced in size; the hypocones are vestigial, a condition which, in view of the generally high grade of organisation of the skull of the animal and of the advanced development of the molars in many Eocene Primates, we may not safely regard as primitive. The roundness of the molar cusps and of the whole crowns is also a retrogressive character in certain other phyla of the Primates, including the human phylum."

"They are extremely progressive in the progressive development of the upper canines."

Vertebral Column.

The vertebral formula is as follows:—

Cervical.....	7
Thoracic	12 or 13
Lumbar.....	7 or 6
Sacral	3
Coccygeal.....	25

The number of thoracic vertebræ varies even within the species *Hapale jacchus*. The pre-coccygeal formula is identical with that of the Marsupials—*Tupaia*, *Tarsius*, and the Lemurs generally. The unstable character of the last thoracic vertebra, sometimes bearing a rib and sometimes becoming a lumbar vertebra, connects the Hapalidæ with the higher Primates. Some of the Cebidæ have a greater number of thoraco-lumbar vertebræ than 19, but within the Hapalidæ the number of thoraco-lumbar remains constant.

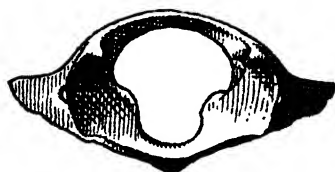
The Atlas.—The ventral arch is narrow and bears a median tubercle on the inferior edge. The articular surfaces for the occipital condyles are sharply marked off posteriorly by a ridge which lies immediately in front of the foramen for the vertebral artery on the internal surface of the posterior arch. This suggests a condition similar to that in *Tarsius*, where the posterior ridge converts the posterior part of the articular surface into a gutter. There is a transverse ligament as in Man, and not a bony bar as in *Tarsius*. The transverse processes are flattened and face downwards and upwards. Close to the junction with the base of the articular process they are perforated by a foramen for the vertebral artery. Running dorsally from within the canal in the transverse process a canal passes backwards to open as described above. The dorsal arch carries no tubercle, but has a ridge along its inferior edge. The inferior articular surfaces are flattened and face inwards and downwards.

The Axis.—The odontoid process is inclined backwards at a sharp angle with the body of the axis. When the axis is held horizontal the odontoid is tilted dorsally almost 45 degrees. The anterior aspect of the process is rounded and articulates with the posterior surface of the ventral arch of the atlas. This anterior

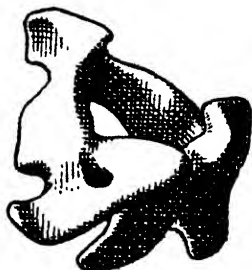
articular surface is separated off by a groove from the articular surface for the inferior articular surfaces of the atlas. The inferior edge of the body of the bone is prolonged downwards into a sharp triangular process which overlaps a considerable portion of the body of the third cervical vertebra. The transverse processes are perforated by a foramen for the vertebral artery. The spine is large and compressed laterally. Its tip is bifid.

The remaining cervical vertebræ possess the downward prolongation of the inferior edge of the bodies. This process becomes gradually smaller as the seventh is approached. The transverse process consists of a thin plate of bone attached to the junction of

Text-figure 14.



A



B

A. The atlas from above.

B. The axis. Antero-lateral view.

the body with the lamina. It divides into two parts—an anterior or costal part which is a process directed laterally and forwards, and a posterior which is directed almost straight backwards. The articular processes carrying the superior articular facet face upwards and backwards. The spine is large. At its tip it is enlarged into a well-developed tubercle. The spines increase in size from the third to the seventh and are never bifid. They are directed dorsally. In Pl. I. the specimen used for this photograph had the third, fourth, and fifth spines broken off.

The thoracic vertebræ number either twelve or thirteen. The anticlinal vertebra is the ninth. The spines of the first and second vertebræ are similar to those of the lower cervical region,

but below this they become flattened from side to side and decrease gradually in height. The transverse processes in the upper part of the thoracic region are flattened and bear on their anterior surface a facet for the articulation of the rib. Posteriorly they form a slight tubercle. In the more distal part of the thoracic region the posterior tubercle is elongated cranio-caudally and forms an upper process and a lower. Below the tenth the ribs do not articulate with the transverse process. The upper process is for the attachment of the cost-transverse ligament, and the lower for muscular attachments. The elevation on the anterior surface of the transverse process in the upper part of the region disappears entirely on the last two rib-bearing vertebræ, and on the one cranial to these the elevation on the transverse process is very small (10th T. Vert.).

The lumbar vertebræ number either six or seven according to the number of ribs. The bodies of these vertebræ are elongated cranio-caudally. On the anterior surface a well-marked ridge running in a cranio-caudal direction is seen. This line is present in the lower five or six thoracic vertebræ, but is more marked in the lumbar region. Lying on either side of this ridge a small nutrient foramen is present. The transverse processes are thin plates of bone directed forwards and slightly laterally. They become wider as the lower members of the series are reached, and there they are prolonged into a superior process. The laminae are broad and carry the superior and inferior articular facets. The superior articular facet is concave and faces backwards and medially. The inferior facet is convex and faces laterally and forwards. Anterior to the articulation of the superior and inferior facets on the laminae there is a well-marked posteriorly-directed process arising from the posterior edge of the lamina. This process is largest in the 17th thoraco-lumbar vertebra, and decreases in size in the anterior members of the series. In the 18th vertebra it is small, and in the 19th is absent. The neural spines are large, flattened from side to side, and are enlarged at their tips into an oval tubercle. The mammillary process of the superior articular processes are well marked in the last three thoracic vertebræ and in all the lumbar series.

The sacral vertebræ are three in number and are fused together into a single bone. The articular area for articulation with the ilium is composed almost entirely by the transverse process of the first sacral vertebræ, the second vertebra taking but a small share in the formation of the joint surface, while the third is entirely excluded. The metapophyses lie close to the base of the neural spine and medial to the foramina. Two foramina are seen—a small anterior between the first and second vertebræ and a large posterior between the second and third. The spines are short; that of the first vertebra is directed forwards, while the posterior two are directed straight backwards.

There are twenty-five tail vertebræ, divided into three coccygeal and twenty-two caudal. The first three vertebræ in the tail

series are well developed, and differ from the remainder in that they possess transverse processes and neural arches. These coccygeal vertebræ have short bodies which carry the flat laterally-directed transverse processes with a superior and an inferior tubercle. The superior auricular process carries a mammillary process. The neural arch is complete in all three vertebræ and terminates at the third vertebra. A hæmal arch was present on the last vertebra, but in the preparation of the skeleton the hæmal arches of the first and second were lost. The arch in the third vertebra was a disc-shaped plate of bone attached along the inferior edge of the vertebra and directed forwards. It was perforated by a small foramen.

The remaining tail vertebræ possess neither neural arches nor transverse processes. They have long cylindrical bodies enlarged at the anterior and posterior ends, where they articulate with each other. The first of this series is short, the second slightly longer, while the third to the tenth are of almost the same length. From the eleventh to termination there is a gradual decrease in length.

Curves of the Vertebral Column.

The cervical curve is concave backwards, but the depth of the curve is very slight. The thoraco-lumbar vertebræ form a continuous arch, concave ventrally. The sacrum is straight. The first three tail vertebræ are free to move considerably in a ventral direction, but the dorsal flexion is limited. The remaining tail vertebræ are fairly free to move in all directions.

The Ribs.

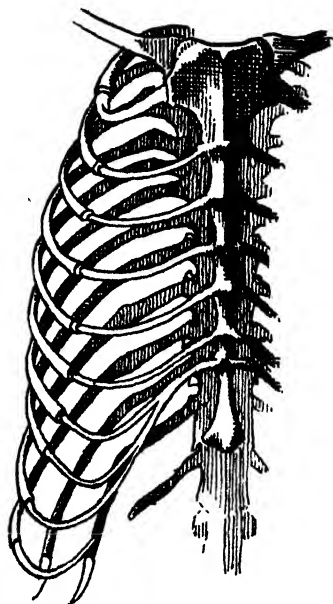
The ribs may number either twelve or thirteen. The first rib is slender, and is compressed from above downwards. It articulates in front with the manubrium sterni and behind with both the body and transverse process of the first thoracic vertebra. The remaining ribs are very slightly convex on the outer surface. The inner surface is divided in two parts—an upper convex and a lower concave. This gives the rib the appearance of bearing a flange along its lower border. In this way the ribs lie closely together and the intercostal spaces are very narrow. Seven ribs reach the sternum. The eighth and ninth costal cartilages may fuse very close to the sternum, but do not reach it. The eighth is often fused with or applied to the under surface of the seventh. The tenth, eleventh, twelfth, and thirteenth (if present) are free.

The Sternum.

The sternum is made up of seven segments. The first, or manubrium, is broad above and narrows below. Laterally it is produced out to the place of articulation of the first rib. Above this point the clavicle is attached. Along the median plane in front there is a well-marked ridge for the attachment of the

pectoralis major. The five succeeding segments are dumb-bell shaped. The costal cartilages meet the sternum at the points of junction of the several segments. The fifth piece is short, and below it is joined to the xiphisternum, which is longer than any of the segments but much thinner. At its distal extremity it is expanded transversely into a cartilaginous plate. Parker states that the fifth segment is made up of two bilateral grains of bony tissue. This condition may occur occasionally, but I have not seen it. All my specimens show a well-developed fifth segment.

Text-figure 15.



The sternum and ribs.

He also remarks that in the Marmoset the xiphisternum is the most expanded of all the Primates. (Text-fig. 15.)

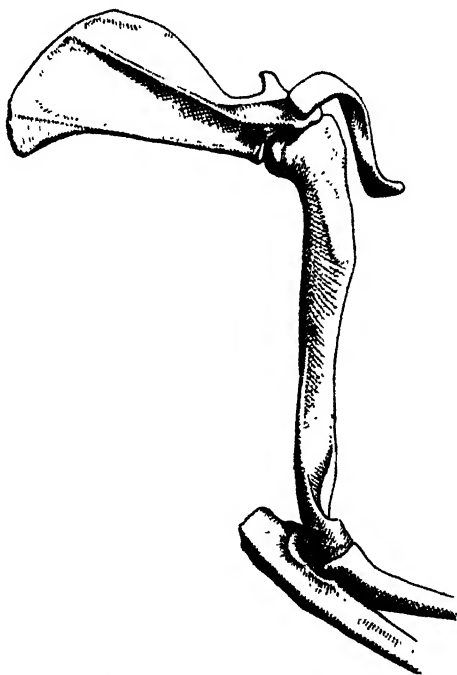
The Shoulder-Girdle and Upper Extremity.

The shape of the *clavicle* is almost exactly that of the human clavicle. The sternal extremity is expanded downwards, so that in cross-section this extremity is almost triangular. To the anterior surface of this expanded area is attached the pectoralis major. The outer extremity is flattened. Parker describes a specimen which had an ossific centre for the outer end which he calls the outer part of the meso-scapular segment. I have not seen a specimen which demonstrates this point, but in one animal

there was a distinct mass of cartilage at the extreme lateral end of the clavicle which may ossify separately.

The scapula is triangular. The outer surface is divided into two unequal portions by the thin bony spine of the scapula. The spine commences a considerable distance from the superior angle, and laterally is produced into the acromial process. The glenoid cavity is shallow and occupies the apex of the triangle. From the apex the coracoid process arises as a thin plate of bone which expands medially and is produced into a slender bar of

Text-figure 16.



The bones of the shoulder-girdle and upper arm.

bone. Lateral to this is a small tubercle for the attachment of the long head of the biceps. The coracoid assists in the formation of the glenoid cavity. The inferior angle of the scapula is rounded and is often cartilaginous.

The *humerus* articulates with the scapula by means of the hemispherical articular surface of the head. The greater and lesser tuberosities are present. The bicipital groove is wide and shallow. Its lateral border is sharp, and to it is attached the pectoralis major. Above, the ridge is continuous with the great tuberosity, while below it forms the medial boundary of the deltoid area.

This area is extensive, but it only extends along the shaft for about one-third of the length of the bone. There is no bony musculo-spiral groove. Below the deltoid area the two epicondylar ridges become prominent and give the bone a flattened appearance. The lateral is more prominent, while the medial is more rounded. There is no epicondylar foramen. In this respect the bone differs from *Tarsius* and all the Lemurs with the exception of *Perodicticus*. The medial epicondyle is large, and on its posterior surface has a shallow groove. The inferior articular surface resembles that of *Tarsius*. The ulnar portion is trochlear in shape. It extends upwards on the anterior surface, and above it is separated from the lower part of the humeral shaft by a very faintly-marked depression. On the posterior surface it is not far distant from the edge of the olecranon fossa. The radial articular facet is globular like *Tarsius*. Above, on the anterior surface there is a distinct fossa, while on the posterior surface the articular surface extends well above that for the ulna. The olecranon fossa is triangular in shape and its floor is very thin.

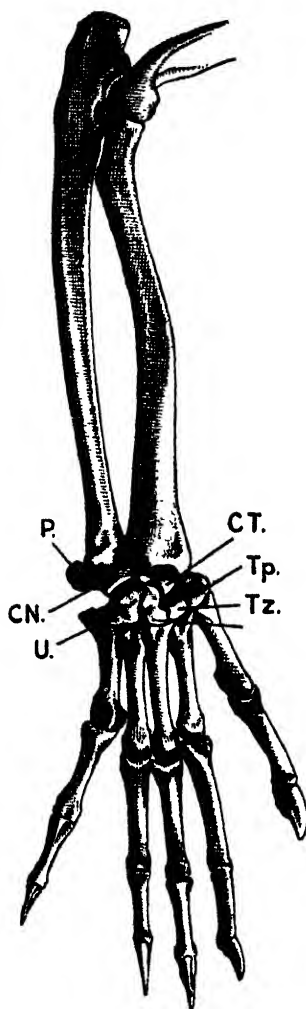
The *ulna* is slightly longer than the humerus. The olecranon is large and possesses a large area for the attachment of the triceps muscle. The articular surface is deeply excavated to produce a distinct anterior and posterior ridge, along which is attached the joint capsule. The surface of the bone for articulation with the radius is continuous with the semilunar articular surface. The former is a small area which lies more on the anterior than on the lateral surface of the bone. The shaft is slightly bowed backwards. The lateral surface of the shaft is concave, while the medial is convex. The posterior surface is narrow and convex. The shaft thins distally, but expands again to form its carpal extremity. On the inner side a small styloid process is formed. There is a small convex surface for articulation with the distal end of the radius.

The *radius* is a much stronger bone than the ulna. It is bowed out laterally and gradually thickens as the distal end is reached. The bone is slightly flattened antero-posteriorly. The head is expanded to form a disc-shaped plate of bone. The upper surface is concave for articulation with the humerus, and on its medial surface there is a wide area for the ulnar articulation. These two areas are continuous. The bicipital tubercle is rounded and relatively long in proportion to its width. The lower extremity is large and has a considerable styloid process. On its palmar surface the extremity is smooth and slightly concave, while the dorsal surface is convex and grooved. The articular area is large.

The carpus consists of nine bones. In their pattern they resemble *Tarsius*, but the proportions of some of the bones differ slightly. The radius articulates with the scaphoid and the lunate; the ulna with the cuneiform and the pisiform. The articular surfaces of these bones with the radius and ulna shows that extension at the wrist can be effected to almost a right angle.

Flexion appears to be only slightly less. The first row articulates with the distal row in the following manner :—the scaphoid with

Text-figure 17.



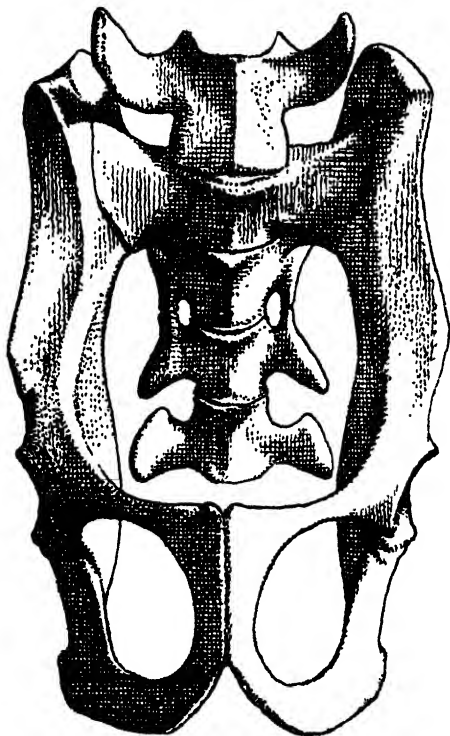
The bones of the forearm and hand.

Cn. Cuneiform. Ct. Centrale. Tp. Trapezium. Tz. Trapezoid. P. Pisiform.
U. Unciform.

the trapezium and with the centrale, which is a large bone considerably larger than the trapezoid. The lunate, which in

Tarsius has a considerable articulation with *centrale*, is articulating mainly with the *os magnum* and the *centrale* articulation is very small. The cuneiform articulates only with the unciform. The *centrale* articulates distally with the trapezoid and slightly with the trapezium. The pisiform is very large. It is wedge-shaped, with the apex inserted between the ulna and the cuneiform. Its large medial mass forms the attachment of the flexor carpi ulnaris.

Text-figure 18.



The pelvis.

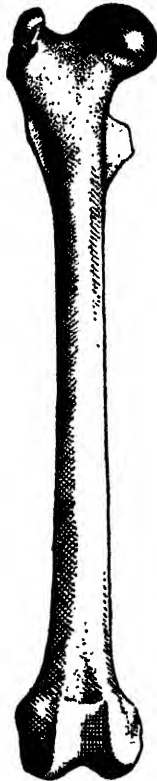
The articulations of the metacarpals with the carpals are shown in text-fig. 17. The bases of the ulnar four metacarpals are bound together by a strong transverse ligament. The heads are joined in much the same manner, but there is more play in the distal ligament. The first metacarpal is of the same length as the fifth and is of equal strength although slightly shorter.

The Lower Extremity.

The innominate bones meet to form a very long symphysis.

The obturator foramen is large and almost circular. The acetabulum is circular, deep, with a wide notch and a very thin floor. The articular surface is C-shaped and extends more over the superior part of the cavity than over the anterior or posterior parts. The ala of the ilium is almost quadrilateral. At its anterior superior apex there is a small tuberosity—the anterior superior spine. Posteriorly the crest is short and narrow and

Text-figure 19.

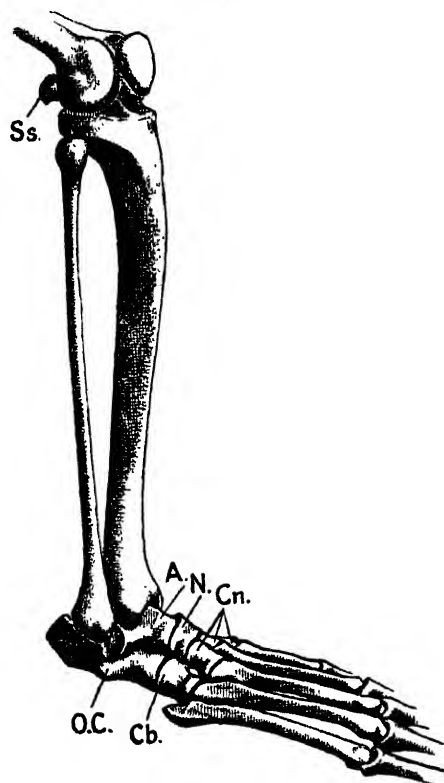


The femur.

terminates in a rounded postero-superior angle. Below this the outer surface of the ala is divided into an outer and inner part by a ridge. The postero-inferior spine marks the distal extremity of the sacro-iliac joint. The anterior inferior spine is blunt but well marked. The inner surface of the ala is divided into three parts by the sacro-iliac joint. The ileo-pectineal line is continued downwards from the ala of the ilium to form the sharp upper edge

of the superior ramus. This ramus of the innominate bone thin, but medially it expands to form the body of the pubis. The inferior ramus is thicker than the superior. Dorsally it expands to form the body of the ischium, from which arises the ischial tuberosity. The tuberosity faces directly backwards, but is not expanded into a plate. It remains narrow across the bone, but is extended in a dorso-ventral direction.

Text-figure 20.



The bones of the leg and foot.

A. Astragalus. N. Navicular. Cn. Cuneiform bones. Cb. Cuboid.
O.C. Os calcis.

The *femur* articulates with the acetabulum by means of a spherical head, which has a fossa for the ligamentum teres. The neck is short and stout. The great trochanter is large and possesses an extensive lateral surface which is prolonged downwards and posteriorly to form a postero-lateral flange on the shaft of the bone. Immediately below the lateral surface and half-way to

the termination of the flange there is a well-marked third trochanter. The small trochanter is well developed. Posteriorly it is continued down by a thin ridge to meet the flange from the great trochanter. They thus form the *linea aspera*, which is really a small area lying between a lateral and a medial line, which lines are continuous below with the supracondylar ridges. The two lines never fuse to form the *linea aspera* which is seen in Man. Lying at the base of the great trochanter on its medial aspect there is a shallow digital fossa. The distal extremity of the bone expands gradually from the smooth rounded shaft. Between the two supracondylar ridges there is a smooth popliteal area. On the lateral condyle there is a small tubercle lying above the upper limit of the posterior part of the articular surface. This is the so-called adductor tubercle. It is the insertion of the *pre semimembranosus*. The medial condyle is larger than the lateral. The articular surface consists of a trochlear surface for the articulation of the patella and on each side of this the two surfaces for the tibial articulation. The posterior parts of the rounded condylar articular surfaces articulate with the sesamoid bones in the heads of the *gastrocnemius* muscle. There is a considerable amount of torsion of the upper extremity of the femur on the shaft and lower extremity. It amounts to about thirty degrees.

The *patella* is a small almost circular bone. There are no proximal and distal patellæ as described in *Tarsius*. It articulates entirely with the femur.

The *tibia* is slightly longer than the femur. The upper surface is described in the account of the knee-joint (see page 678). The upper part of the shaft is triangular in cross-section, but at the middle it becomes almost circular and then expands again to form the inferior extremity. The medial malleolus is large with a deep groove on its posterior aspect for the flexor tendons. The fibula articulates above with the upper extremity of the tibia on its lateral surface. It takes no part in the formation of the knee-joint. It is a thin bone, almost circular in section throughout the whole of its course. The lower extremity forms the lateral malleolus and is attached to the tibia by strong ligaments. There was no bony fusion in this region in the specimens which I examined. The head is large and rounded, with a small tubercle on the lateral aspect for the attachment of the fibular collateral ligament.

The tarsal bones are much more primitive than those of *Tarsius*. In *Hapale* the foot is long owing to the great lengthening of the metatarsals, whereas in *Tarsius* the tarsals are elongated. The foot as a whole, from the tuberosity of the *os calcis* to the tip of the third digit, is almost equal to the length of the femur. The general arrangement of the tarsus and its articulations resemble very closely the condition described by Le Gros Clark in *Ptilo-oercus*.

The *astragalus*.—The articular surfaces which take part in the

formation of the ankle-joint are three in number and are separated from each other by ridges. The lateral surface of the body of the bone is entirely articular. The surface is a broad crescent with a shallow concavity. This surface articulates with the lateral malleolus. Medially a sharp ridge separates the fibular surface from the upper articular surface. This surface is shaped like a pulley into the concavity of which the ridge on the lower articular surface of the tibia fits accurately. This surface extends forwards to reach the base of the neck of the bone and posteriorly almost as far as the articulation with the *os calcis*. Medially the upper surface is divided from the medial portion of the upper articular surface by another sharp ridge. The medial surface is slightly convex and extends forwards for more than half the length of the neck of the bone. It is obvious that the extent and the formation of the articular surfaces are to provide a wide range of movement at the ankle-joint, especially dorsiflexion. The neck is a constricted shaft of bone six millimetres in length and expanding to form the rounded head of the bone. The articular surface of the head forms more than half a sphere, but the main part of the articular surface faces downwards and forms part of the anterior astragalo-calcanean articulation. The anterior surface is received into the deep excavation on the posterior surface of the navicular. The posterior astragalo-calcanean joint is formed by the semilunar articular surface of the astragalus which articulates with the convex upper articular surface of the *os calcis*. This inferior articular surface of the astragalus covers the whole of the inferior surface of the body of the bone and the anterior three-fourths of the inferior surface of the neck. In front of the body along the under surface of the neck there is attached a strong astragalo-calcanean ligament which binds the astragalus to the *os calcis* and occupies the whole of the wide tarsal tunnel. The axis of the neck is inclined to the antero-posterior axis of the body at an angle of about 30 degrees. The neck lies in the long axis of the foot, and consequently there is normally an external rotation of the whole limb at the hip-joint.

The fibular collateral ligament is attached to the postero-inferior angle of the lateral surface of the body. The posterior surface of the body is grooved for the flexor fibularis tendon.

The *os calcis* has four articular surfaces. The posterior surface is oval and divided into two parts—an upper smooth area for the bursa beneath the tendo Achillis and a lower area which is rough for the attachment of the tendon. The posterior area passes into the inferior surface imperceptibly. The inferior surface is rough over the more posterior part, for the attachment of the accessory head of the flexor digitorum brevis. The anterior portion is smooth and rounded. It passes insensibly into the medial and lateral surfaces. On the lateral surface there is a prominent peroneal tubercle which is smooth and not

grooved. The medial surface is deeply excavated between the sustentaculum tali and the posterior surface of the bone. This groove is converted into a tunnel by a strong ligament attached to the medial edge of the posterior surface of the bone and above to the medial surface of the astragalus. The sustentaculum is a broad transverse shelf projecting medially with its upper or dorsal surface concave for the articulation of the inferior surface of the astragalus. Posterior to the facet on the sustentaculum is the convex articular surface for the inferior astragalo-calcaneal articulation. The anterior articular surface for the cuboid is concave in all directions. The surface of the bone immediately posterior to the cuboid articular surface is smooth, and to it is attached the origin of the extensor digitorum brevis muscle.

The *scaphoid*.--The posterior articular surface for the articulation of the astragalus is pear-shaped. The apex points upwards and laterally. To the lateral side of this the bone articulates with the cuboid by means of a small triangular facet. In front the three cuneiform bones articulate. The surface for the lateral cuneiform is concave. The surface for the medial cuneiform is convex and is the largest of the three. The middle bone articulates over a very small area which is flat. The tuberosity of the scaphoid is blunt and rounded.

The *cuboid* has a convex surface posteriorly for the os calcis and a small medial surface for the scaphoid and the postero-lateral angle of the lateral cuneiform. In front there is a narrow area for the articulation with the bases of the fourth and fifth metatarsals. The plantar surface is deeply grooved for the peroneus longus. The antero-medial angle of the bone bears a small articular surface for the antero-lateral angle of the lateral cuneiform.

The *lateral cuneiform* (*ectocuneiform*) is a quadrilateral bone articulating posteriorly with the most lateral part of the scaphoid. This surface is convex. Anteriorly and on its medial side the second metatarsal articulates with the bone. The anterior surface is oblique and is flat for the base of the third metatarsal.

The *middle cuneiform* (*mesocuneiform*) is the smallest of the series. It is slightly constricted in the middle and has a slightly convex surface for the scaphoid. Anteriorly it articulates with the second metatarsal.

The *lateral cuneiform* (*entocuneiform*) is the largest of the three bones. It is prolonged posteriorly into a blunt rounded apex which articulates with the under surface of the scaphoid. It does not reach as far posteriorly as the astragalus. The plantar surface bears a strong ridge to which is attached the strong plantar fascia. The anterior surface is notched to receive the ridge on the base of the first metatarsal. Laterally the bone articulates with the base of the second metatarsal and with the mesocuneiform. There is no trace of a pre-hallux.

The *first metatarsal* is considerably shorter than the remaining members of the series. Its base bears a ridge which runs

dorso-ventrally and separates the articular surface into two parts each of which is concave. The tuberosity on the ventral or plantar aspect of the base is a low prominence, and to it is attached the peroneus longus tendon. The proximal phalanx is shorter than the same bone in the other digits. The terminal phalanx is flattened and short. This is correlated with the flat nail which this digit bears. The other metatarsals have strong shafts. The fifth is the weakest. On its base the lateral side of the bone is prolonged into a strong tuberosity. Abduction and adduction of the fifth metatarsal can be effected through a considerable range, judging from the wide interval between the tuberosity of the bone and the cuboid.

THE MUSCULAR SYSTEM.

The cutaneous musculature of *Hapale* shows considerable reduction when compared with the Lemuroid and the Tarsioid condition. The continuous sheet of fibres—the panniculus carnosus—which is present in *Tarsius* has become broken into two distinct parts. The anterior part is confined to the axillary region. Numbers of muscle fibres are seen to lie in the fascial plane connecting the lateral edge of the pectoralis major with the anterior edge of the latissimus dorsi. These fibres converge on the apex of the axilla and are inserted into the fascia covering the coraco-brachialis and eventually into the humerus. In this they are homologous with the Achselbogen of Man. The posterior part of the panniculus carnosus has persisted and has become divided into two parts, a medial and lateral dorso-lumbar group of fibres. The medial group is a thin sheet of fibres which lie over the dorsal part of the body-wall in the lumbar region and are continued downwards towards the tail. They fade out laterally and over the sacral region. The lateral group of fibres is a mass of fibres which arise in the lower dorsal region and sweeping laterally and downwards pass into the thigh to reach its medial side. The fibres end about the region of the knee.

The most anterior part of the cutaneous musculature is described under the facial musculature. There is no apparent continuity between the axillary sheet of muscle and the platysma nor between the dorso-lumbar sheet and the posterior part of the platysma. In this respect the condition found in *Hapale* closely resembles the Anthropoid arrangement.

The work of Ruge on the Achselbogen in Man summarises the conditions in most of the Primates, but he does not figure the *Hapale* sheets.

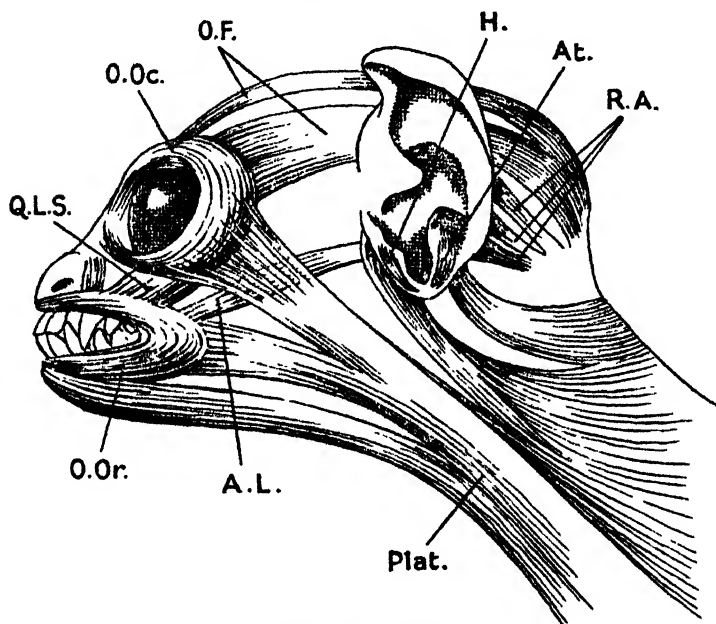
Facial Musculature.

It has not been possible to obtain satisfactory serial sections of the anterior part of the face to settle points of doubt in the description of these muscles. The descriptions of the muscles are based on the dissection of a fresh and a preserved specimen.

The fresh specimen was used to confirm as far as possible the conclusions reached in the original description.

Platysma.—The platysma is not nearly so well defined as Woollard has described for *Tarsius*. The sheet is very thin over the posterior neck region and the middle line of the neck, in front. A fairly well-defined mass can be made out which runs from the fascia over the pectoralis major to the face in the region of the angle of the jaw. This sheet thins out anteriorly and posteriorly. The posterior fibres tend to run almost directly

Text-figure 21.



The facial musculature.

A.L. Auriculo-labialis. At. Antitragicus. H. Helicis. O.F. Occipito-frontalis. O.Oc. Orbicularis oculi. O.Or. Orbicularis oris. Plat. Platysma. Q.L.S. Quadratus labii superioris. R.A. Retrahens auris and auriculo-occipitalis.

backwards to the middle line at the back. The anterior fibres thinning out as they near the middle plane cross the median plane only in the sub-mental region. These anterior fibres tend to pass upwards into the lower lip. The clavicular part of the platysma as it reaches the angle of the jaw splits into three well-marked slips. The most anterior passes forward and is inserted into the angle of the mouth and the skin of the lower lip. The middle division runs upwards and blends with the orbicularis oculi. The third division passes backwards and is inserted into the auriculo-labialis and the base of the pinna.

anteriorly. Just before appearing on the face a few fibres pass backwards into the muscles behind the ear. In all these points the general similarity with the *Tarsius* condition is striking.

Sphincter colli profundus.—This muscle is present. It lies deep to the platysma over the upper part of the neck and runs from the base of the ear to the middle line of the neck.

Occipito-frontalis M.—This muscle forms a sheet of muscle which arises from the skin and the subjacent bone along the supra-orbital margin. The fibres pass backwards. Some are inserted into the nuchal line and some become continuous with the platysma. The slips which reach the nuchal line are lying on a deeper plane than the others. These slips have various origins.

(a) A well-marked band arises from the skin above the root of the nose and passes backwards over the skull to be inserted into the superior nuchal line.

(b) Some fibres arising from the lateral part of the orbicularis oculi follow the same course and are inserted lateral to the former group.

(c) The third and smallest band arising from the posterior part of the pinna pass backward into the nuchal line. This band of fibres represents the auriculo-occipitalis and the retrahens aurem. The band does not show any division into two or three divisions as in *Tarsius*.

Orbicularis oculi M.—This complex muscle is made up of slips from the adjacent muscles and from intrinsic fibres. It is a very thin band of tissue which extends almost from the free edge of the eyelids to the edge of the orbit. Fibres arise from the maxilla and the lachrymal bones near the inner canthus of the eye, but also where the insertions and origins of the fibres is in skin. Fibres reach the orbicularis oculi from the occipito-frontalis, the auriculo-labialis, the platysma, and the orbicularis oris.

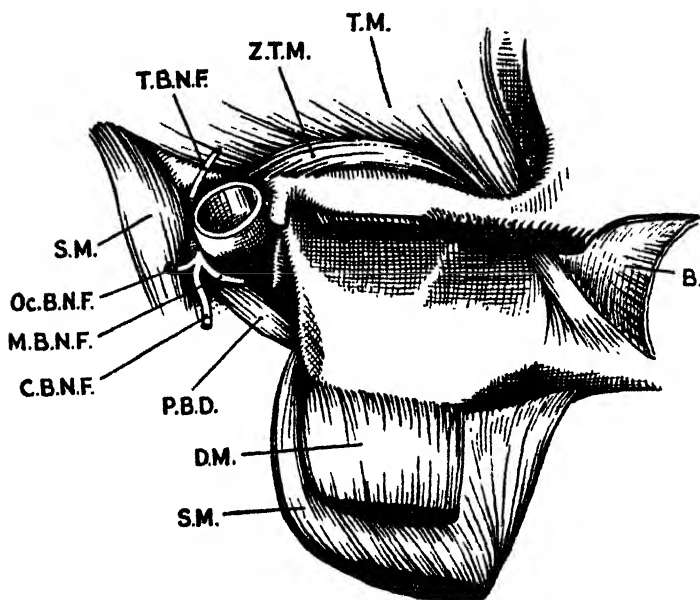
Auriculo-labialis M.—This muscle cannot be subdivided into three parts which are present in *Tarsius*. In the Marmoset it appears to be a single mass of fibres which stretches forwards from the base of the pinna near the incisura. The fibres are inserted into the orbicularis oris and oculi.

Orbicularis oris M.—The orbicularis like the orbicularis oculi is a complex of intrinsic and extrinsic fibres. The intrinsic muscle fibres are circular in their course and are inserted into the skin around the angles of the mouth and the free margins of the lips. The extrinsic fibres belong to two planes—a superficial plane, the fibres reaching the muscle in this plane are from the platysma and from the orbicularis oculi, and a deep layer—the fibres of the auriculo-labialis reach the muscle in this plane which is deep to the platysma group. In the lower lip the fibres of the platysma enter the muscle direct. These fibres are from the platysma anterior to the so-called clavicular portion

described above. It was not possible to determine the presence of a *musculus labialis proprius*. In the deep layer the buccinator sends some fibres into the muscle. These are inserted into the angle of the mouth.

Quadratus labii superioris M.—This muscle appears to be arranged in a manner closely resembling that found in *Tarsius*. The fibres in *Hapale* are very hard to separate out from the orbicularis oris, into which they are inserted.

Text-figure 22.



The muscles of mastication.

T.M. Temporal M. Z.T.M. Zygomatic fibres of temporal muscle. T.B.N.F. Temporal branch of facial nerve. Oc.B.N.F. Occipital branch facial nerve. C.B.N.F. Cervical branch facial nerve. M.B.N.F. Mandibular and maxillary trunk of facial nerve. P.B.D. Posterior belly of digastric muscle. S.M. Superficial fibres of masseter M. D.M. Deep fibres of masseter muscle. B. Buccinator M.

Muscles of Mastication.

M. Buccinator arises from the anterior third of the zygomatic arch and the superficial surface of the maxilla. The posterior fibres lie deep to the anterior margin of the masseter, and the anterior fibres lie deep to the posterior part of the orbicularis oris, into which muscle a number of the anterior fibres are inserted. The fibres sweep down from the origin and incline forwards to be inserted into the mandible along the line of the

reflection of the mucous membrane of the mouth from the bone. The posterior limit of the insertion is immediately behind the third molar tooth. From this point the superior constrictor of the pharynx also arises. The pterygo-mandibular raphe affords origin to the most posterior fibres of the buccinator. These fibres have an almost vertical course into the mandible in the region of the molar teeth.

M. Temporalis.—This muscle arises from the lateral surface of the skull inferior to the temporal line and from the line itself. The line passes backwards almost to the lambda, where it diverges laterally and runs superior to the superior nuchal line, with which it coalesces as far as the temporo-occipital articulation. Fibres arise from the squamous temporal above the external auditory meatus along the posterior root of the zygoma. All the fibres converge on the coronoid process, and in the midst of the muscle mass only a very few tendinous fibres are seen. The fibres which come from the most anterior part of the origin of the muscle along the posterior or temporal surface of the orbital process of the malar bone pass almost vertically downwards, become tendinous and are inserted into the whole of the anterior edge of the ramus of the mandible.

The most posterior fibres from the posterior root of the zygoma do not form a tendon into which the other fibres of the muscle are inserted. In the female the muscle is much less extensive on the lateral surface of the skull. It does not approach the lambda so closely as in the male, nor does it coalesce with the superior nuchal line except at the asterion.

These posterior fibres form a large part of the muscle and appear to be specialised to give an antero-posterior pull on the coronoid process and to produce a grinding action of the lower teeth on the upper.

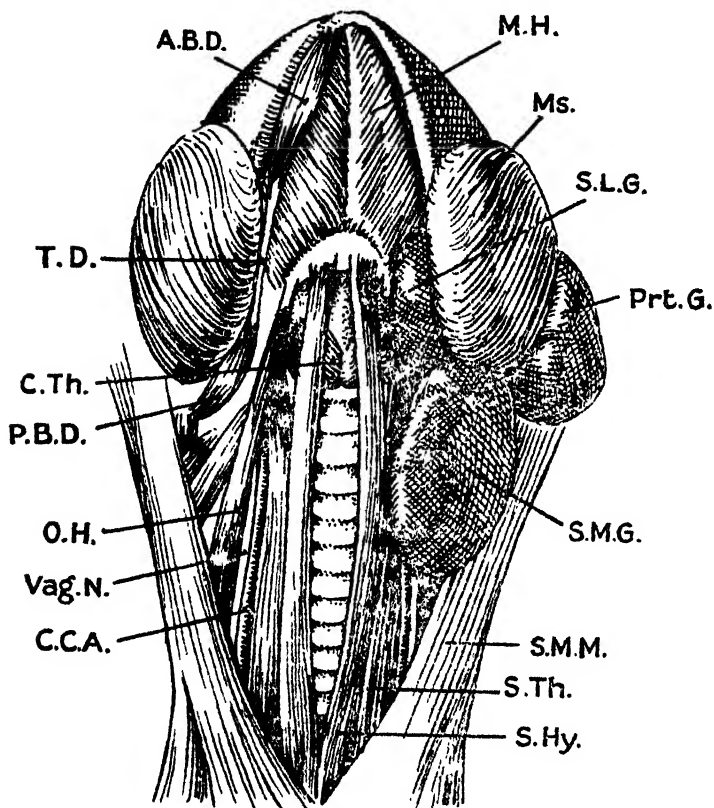
M. Masseter arises by two origins—(a) from the posterior three-fourths of the inferior edge of the zygomatic process, (b) from the whole of the deep surface of the zygoma. The superficial part is inserted into the angle and the lower border of the mandible and along the inferior half of the posterior edge of the ramus. Some of these fibres are inserted into the lower half of the lateral surface of the ramus and become blended there with the insertion of the deep part, which is inserted into almost the whole of the upper half of the outer surface of the ramus above the insertion of the superficial part. The anterior fibres of the deep portion of the muscle blend with the tendinous insertion of the anterior fibres of the temporalis along the anterior edge of the ramus.

M. Pterygoideus Internus arises from the whole of the fossa between the two wings of the pterygoid process of the sphenoid. It descends obliquely backwards and runs along the inferior border of the auditory bulla to be inserted into the deep surface of the angle of the jaw. The fibres arise from a small area, as the pterygoid fossa in the Marmoset is a very small depression

and consequently the origin is tendinous. There is no intramuscular tendon as has been described in *Tarsius*.

M. Pterygoideus Externus.—This muscle is distinctly smaller than the internal pterygoid. It arises from the superficial for

Text-figure 23.



The anterior region of the neck.

A.B.D. Anterior belly of the digastric muscle. P.B.D. Posterior belly of the digastric. T.D. Tendon of the digastric muscle. C.Th. Crico-thyroid muscle. O.H. Omohyoid muscle. Vag.N. Vagus nerve. C.C.A. Common carotid artery. M.H. Mylo-hyoid muscle. Ms. Masseter. S.L.G. Sublingual gland. Prt.G. Parotid gland. S.M.G. Sub-maxillary gland. S.M.M. Sterno-mastoid muscle. S.Th. Sterno-thyroid muscle. S.Hy. Sterno-hyoid muscle.

lateral surface of the external surface of the pterygoid lamina and from the orbital plate of the malar bone posterior to the inferior orbital fissure and along the articulation of the maxilla

with this part of the malar bone. It has thus the same relations as in *Tarsius* except that the malar bone has extended inwards and has separated it from the floor of the orbit. The muscle is inserted into the anterior edge of the condyloid process of the mandible, the intra-articular fibro-cartilage, and the anterior part of the joint capsule.

The digastric and the mylo-hyoid are described with the anterior muscles of the neck.

Muscles of the Neck.

Sterno-cleido-mastoideus M.—This muscle is double in the Marmoset. The lateral portion or the cleido-occipitalis arises from the medial end of the clavicle. It runs backwards and upwards and is inserted into the superior nuchal line. Its posterior border does not come into contact with the trapezius. The medial portion or sterno-mastoid arises from the anterior surface of the first piece of the sternum and coursing backwards it is inserted into the mastoid process. The two portions are of equal size. They are supplied by the spinal accessory nerve.

Omo-hyoid M.—Arising from the upper border of the scapula near its outer end the fibres pass upwards and medially deep to the two parts of the sterno-cleido-mastoid and is inserted into the lateral part of the hyoid bone. There is not a clear demarcation into parts as is seen in the higher primates. The intermediate tendon consists of a few very ill-marked fibres.

Sterno-hyoid M.—The origin of this muscle from the deep surface of the first portion of the sternum lies close to the middle line. The fibres run upwards close to the middle line of the neck and are inserted into the hyoid bone close to the medial plane, on the anterior surface.

Sterno-thyroid M.—Lateral to the origin of the sterno-hyoid the fibres of the sterno-thyroid take origin. The muscle lies parallel to but on a slightly deeper plane to the former muscle. It is inserted into the lateral surface of the hyoid bone along the lowest part of the expanded body of the bone. It lies deep to the sterno-hyoid.

Thyro-hyoid M.—This muscle arises from the upper border of the lateral line on the thyroid cartilage and is inserted into the hyoid bone deep to the omo-hyoid and the lateral part of the sterno-hyoid.

Digastric M.—The anterior belly of the digastric arises from the symphysis menti and the lower edge of the mandibular ramus as far laterally as the most medial part of the insertion of the masseter muscle. Some of the anterior fibres cross the middle line. The posterior limit of this decussation is tendinous. The posterior belly arises from the mastoid area on its deeper surface; some of the fibres are attached to the styloid process. The intermediate tendon is well marked. It is not attached to the hyoid. The tendon lies close to the angle of the jaw. The course of the muscle is almost straight from the symphysis menti to the

mastoid process. The anterior belly is supplied by the hypoglossal nerve and the posterior belly by a slip from the facial nerve.

Mylo-hyoid M.—The mandibular origin of this muscle lies deep to the anterior belly of the digastric along the inner surface of the mandible from the symphysis to the anterior margin of the insertion of the masseter muscle. The anterior fibres are inserted into a median raphe which extends backwards to be inserted into the hyoid bone. The posterior fibres curve backward and some of them are attached directly into the hyoid.

Genio-hyoid M.—The fibres of this muscle arise from the upper border of the hyoid and running forward are inserted into the mandible close to the symphysis menti.

Hyoglossus M.—This is a fan-shaped muscle which arises from the hyoid near the middle line. The fibres expand as they run upwards and are inserted into the tongue. Some of the anterior fibres appear to get an attachment to the mandible in the region of the symphysis. There is no separation from the main mass of the muscle to justify the description of a separate genio-hyoglossus muscle. The lingual artery lies deep to the hyoglossus.

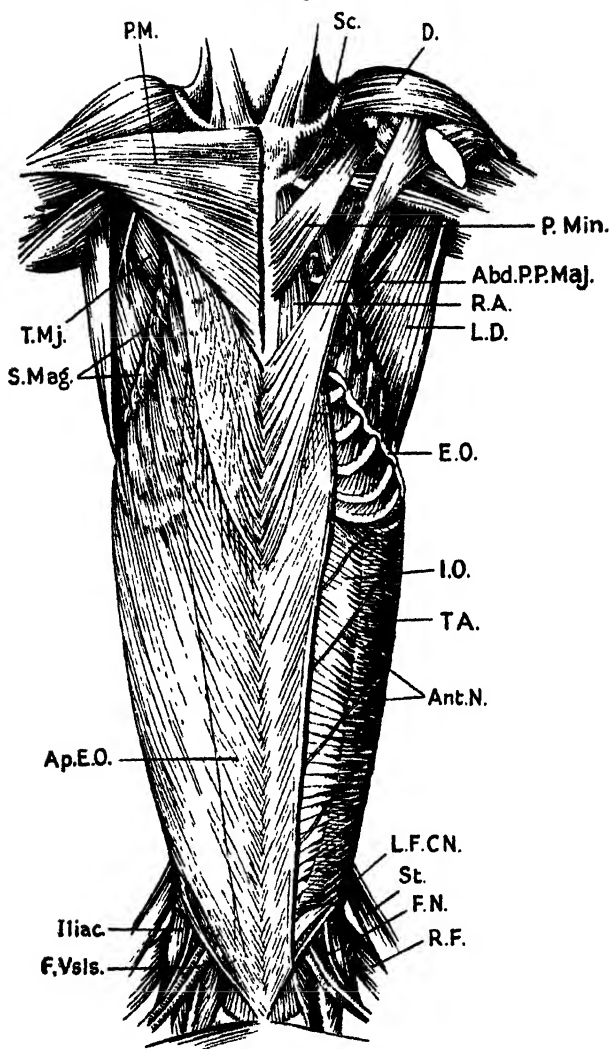
The Pre-vertebral Muscles.

M. Rectus Capitis Anticus Major.—This is a very extensive muscle which arises from the anterior tubercles of the fourth, fifth, and sixth and sometimes the seventh cervical vertebræ. It forms a large mass of muscle which is inserted into the basi-occipital along with its fellow of the opposite side between the anterior ends of the auditory bullæ.

M. Rectus Capitis Anticus Minor.—This muscle arises from the body and transverse processes of the atlas and forms a thin quadrilateral muscle which is inserted into the basi-occipital posterior to the insertion of the former muscle.

M. Longus Colli can be divided into three parts as in all the higher primates and described by Woollard in *Tarsius*. The lower oblique part arises from the lateral aspect of the bodies of the upper two or three thoracic vertebræ. It inclines laterally and is inserted into the transverse processes of the fifth and sixth cervical vertebræ. The upper oblique portion arises from the anterior tubercles of the third, fourth, and fifth cervical vertebræ and inclines medially to be inserted into the anterior tubercle of the atlas. The vertical part of the muscle arises from the upper two or three thoracic vertebræ in common with the lower oblique part to its medial side. The muscle passes up into the neck, and after obtaining a few slips from the anterior surfaces of the lower two or three cervical vertebræ it is inserted into the anterior surfaces of the bodies of the upper four cervical vertebræ. The slip to the anterior tubercle of the atlas is a thin tendon which fuses with the medial edge of the upper oblique portion of the muscle.

Text-figure 24.



The anterior muscles of the trunk.

P.M. Pectoralis major M. **Sc.** Subclavius M. **D.** Deltoid M. **P.Min.** Pectoralis minor M. **Abd.P.P.Maj.** Pars abdominalis of pectoralis major M. **R.A.** Rectus abdominis M. **L.D.** Latissimus dorsi M. **E.O.** External oblique M. **I.O.** Internal oblique M. **T.A.** Transversus abdominis M. **Ant.N.** Anterior divisions of lower intercostal nerves. **L.F.C.N.** Lateral femoral cutaneous nerves. **St.** Sartorius M. **F.N.** Femoral nerve. **R.F.** Rectus femoris M. **F.Vls.** Femoral vessels. **Iliac.** Iliacus M. **Ap.E.O.** Aponeurosis of external oblique M. **S.Mag.** Serratus magnus M. **T.Mj.** Teres major.

The Scalene Muscles.

M. Scalenus Anticus arises from the transverse processes of the fifth and sixth cervical vertebræ and is inserted into the anterior surface of the medial end of the first rib. It passes deep to the subclavian artery and superficial to the brachial plexus.

M. Scalenus Medius and *M. Scalenus Posticus*.—These two muscles separate in Man are fused and form a single large sheet of muscle fibres lying behind the brachial plexus. The muscle arises from the transverse processes of the second to the sixth cervical vertebræ and passing downwards spreads outwards on the lateral surface of the thorax and is inserted into the lateral surface of the upper four ribs.

The Vertebral Region. (Posterior and superior.)

Splenius capitis M.—The origin of this muscle is from the ligamentum nuchæ, the spines and interspinous ligaments of the last cervical and the upper two thoracic vertebræ. It is inserted into the superior nuchal line from the median plane to the mastoid process.

Splenius cervicis M.—Two small slips detach themselves off from the main splenius capitis mass and running laterally are inserted into the transverse processes of the first and second cervical vertebræ.

Complexus M.—This muscle lies deep to the splenius muscles. It arises from the transverse processes of the third, fourth, and fifth thoracic vertebræ and running medially splits into two divisions—a medial and a lateral. Each possesses a single tendinous intersection. They are inserted separately into the occipital bone below the nuchal line near the median plane.

Trachelo-mastoid M.—A thin slip of muscle arises from the second, third, and fourth thoracic vertebræ and is inserted into the occipital bone and the mastoid process. The origin of the muscle is much lower than the same muscle in *Tarsius* and is inserted into the occiput much more lateral than the *Tarsius* muscle.

M. Rectus Capitis Posterior Major arises from the spine of the axis and is inserted into the squamous part of the occipital bone along the lateral portion of the bone. It is a triangular muscle, and is very strong in *Hapale*.

M. Rectus Capitis Posterior Minor lies to the medial side of the major and is overlapped by it. It arises from the tubercle of the posterior arch of the atlas and is inserted into the medial part of the squamous occipital.

M. Obliquus Capitis Superior arises from the transverse process of the atlas and is inserted into the occipital bone in the interval between the nuchal line and the semi-spinalis capitis.

M. Obliquus Capitis Inferior arises from the spine of the axis

and is inserted into the transverse process of the atlas. The great occipital nerve hooks round its inferior border.

These muscles are small and weak.

Muscles of the Trunk.

The supra-costal muscles.—These muscles are not present in the Marmoset.

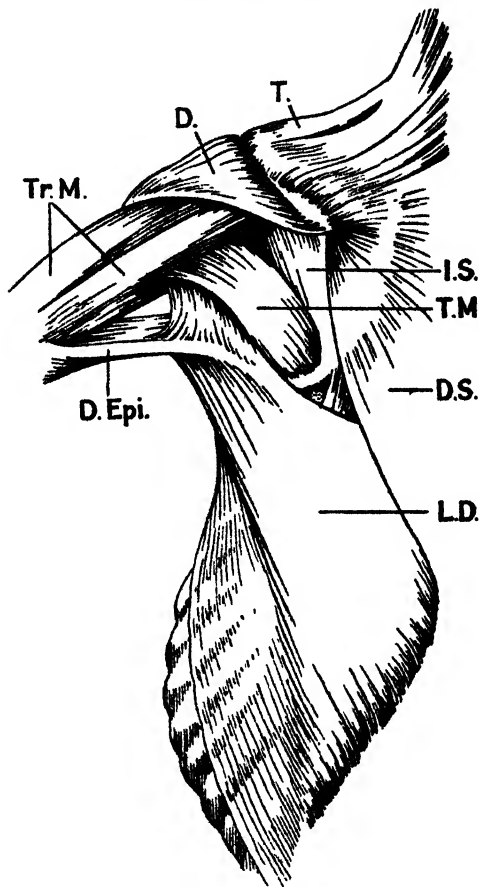
External oblique M.—The external oblique muscle arises from a series of muscular slips from all the ribs. In the upper six ribs the origin corresponds to the junction of the costal cartilage with the rib. Below the sixth rib the origin becomes more and more posterior, shifting on to the rib itself. The posterior fibres of the muscle which arise from the last rib are attached by strong fascia to the posterior lamella of the lumbo-dorsal fascia. This same fascia binds these fibres to the crest of the ilium. At the anterior superior spine of the ilium the lower muscle fibres obtain an attachment to that bone. The main fibres run downwards and inwards to gain attachment to the linea alba by means of an aponeurotic sheet. The muscle fibres in the lower and medial part of the muscle arch in a crescentic manner to form the superior edge of the external abdominal ring. These fibres are concentrated into a well-marked pillar of muscle and tendon which is inserted into the body of the pubis. This tendinous mass forms the medial boundary of the external abdominal ring. The fascial sheet which lies below the lower muscular fibres becomes pulled out over the spermatic cord to form the external spermatic fascia. The medial pillar of insertion lies free of the anterior sheath of the rectus muscle.

Internal oblique M.—The origin of the internal oblique is from the lumbo-dorsal fascia, the outer third of the crural arch, and from the anterior superior spine of the ilium. The muscle slips do not become tendinous until just before they reach the lateral edge of the rectus muscle. Above the origin from the lumbo-dorsal fascia the muscle fibres are continuous with the external intercostal muscles of the eleventh and twelfth spaces. The aponeurotic insertion splits to enclose the rectus muscle as far down as the mid-joint between the umbilicus and the pubis. Below the latter point the whole of the tendon of insertion of the internal oblique lies in front of the rectus.

Transversalis abdominis M.—The fibres of this muscle take origin from the lumbo-dorsal fascia, the costal cartilages, and the ribs from the seventh to the twelfth. Some fibres arise from the iliac crest and from the lateral two-thirds of the crural arch. The upper fibres run transversely with a slight inclination downwards and are inserted into the linea alba and bear the same relation to the rectus muscle as the internal oblique. Like the internal oblique the lower fibres form a low arch over the spermatic cord. The fibres of the cremaster muscle are derived mainly from the transversalis.

Rectus abdominis M.—The origin of the rectus is over a wide area of the body and superior ramus of the pubis and on to the iliac part of the pubic ramus. It is a broad strap-like muscle

Text-figure 25



The muscles of the scapular region.

T. Trapezius. D. Deltoid. Tr.M. Triceps. D.Epi. Dorso-epitrochlearis. T.M. Teres major. I.S. Infraspinatus. D.S. Depressor scapulae. L.D. Latissimus dorsi.

which runs along the ventral surface of the abdomen without any sign of tendinous intersection. The medial fibres of the muscle appear to blend with the upper fibres of the external oblique arising from the upper ribs, and hence it is possible that

the muscle may be inserted as far cranial as the first rib. The lateral part of the muscle is inserted into the costal cartilages of the ribs as low as the ninth costal cartilage. The pyramidalis muscle is not separated off as a distinct muscle mass in the Marmoset. As Woollard has noted in *Tarsius*, some of the lateral fibres of the muscle run medially into the linea alba. This cannot be shown in the Marmoset.

M. Triangularis sterni arises from the deep surface of the sternum and the xiphoid process as high as the second rib. The muscle is composed of a series of slips which diverge laterally to be inserted into the deep surface of the second to the seventh ribs.

The Dorsal Region.

Trapezius M.—This muscle is divided into two distinct parts, a supra and an infra spinous. The upper or supra-spinous portion arises from the ligamentum nuchæ as far cranial as the third cervical vertebra. At the level of the seventh the fibres arise from the spines and inter-spinous ligaments to about the level of the fourth thoracic vertebra. All these muscle fibres form a triangular mass of fibres which are inserted into the superior edge of the spine of the scapula along the vertebral two-thirds of its length. The infra-spinous portion arises from the spines and interspinous ligaments of the fourth to the ninth or tenth thoracic vertebra. This portion is inserted into the vertebral half of the lower border of the scapular spine. It forms a very small part of the whole muscle. The nerve supply is from the cervical plexus, and the upper part seems to have a distinct supply from the accessory nerve. The nerve supply to the lower part cannot be demonstrated by dissection. The infra-spinous portion corresponds to the depressor scapulæ which is present in *Tarsius* and absent in the Lemuroidea.

Rhomboides M.—This muscle is divisible into two parts as in Man. It arises from the lower half of the ligamentum nuchæ and the upper three thoracic vertebra and is inserted into the lower half of the vertebral border of the scapula.

Rhomboides capitis M.—This muscle consists of two slips. The more lateral slip arises from the occiput just lateral to the middle line and runs downwards and outwards to be inserted close to the other slip at the superior angle of the scapula. The medial slip arises from the ligamentum nuchæ from the level of the fourth to the seventh cervical vertebra, and is inserted into the superior angle of the scapula and the upper two-thirds of the vertebral border.

Levator scapulæ anticus M. arises from the ventral surface of the atlas and is inserted into the acromion. It appears from under cover of the sterno-mastoid as it passes downwards to its insertion. It is not inserted into the clavicle.

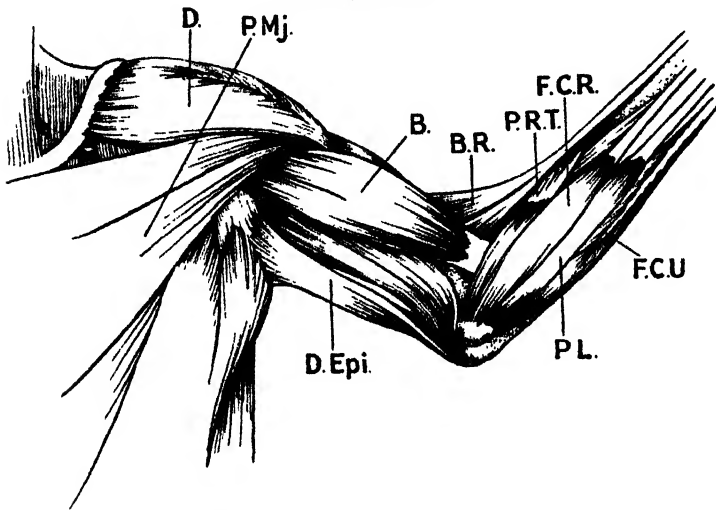
Levator angulæ scapulæ M.—This muscle arises from the transverse processes of the third, fourth, and fifth cervical

vertebræ. The slips form a thick mass of muscle which is inserted into the superior angle of the scapula and along the vertebral border for a short distance.

Serratus magnus M.—The muscle arises from the first to the eighth rib in the mid-axillary line. The upper slips are extremely thin, and the only large muscle masses are from the lower three origins. The fibres are inserted along the whole of the vertebral border of the scapula, but the main insertion is the lower third of the vertebral border.

Serratus posterior superior M.—This muscle could not be

Text-figure 26.



The muscles of the upper arm and the forearm flexors.

D. Deltoid M. P.Mj. Pectoralis major M. B. Biceps. D.Epi. Dorso-epitrochlearis M. B.R. Branchio-radialis M. P.R.T. Pronator radii teres M. F.C.R. Flexor carpi radialis M. F.C.U. Flexor carpi ulnaris M. P.L. Palmaris longus M.

defined. It appears to arise by a very thin aponeurosis from the seventh cervical spine and the spines of the upper three thoracic vertebræ and to be inserted into the upper three or four ribs.

Serratus posterior inferior M.—Like the above muscle this muscle is ill-defined. It overlies the lower four or five ribs.

Sacro-lumbalis M.—This muscle splits off from the erector spinæ mass above the level of the last rib and is inserted into all the ribs along the line of the inferior angle of the scapula.

Cervicalis ascendens M.—This is a very thin slip of muscle which gains insertion into the transverse process of the seventh cervical vertebra.

Longissimus dorsalis M.—This section of the erector spinæ is inserted into the transverse processes of the lumbar vertebræ, the transverse processes and the articular processes of the thoracic vertebræ and small slips into the tubercles of the ribs from the third to the twelfth.

Transversalis cervicis M.—This muscle arises from the same mass of muscle as the previous muscle. It is inserted by six slips into the transverse processes of the second to the seventh cervical vertebræ.

The other muscular masses of the erector spinæ are ill-defined and not possible to describe accurately in such a small animal as the *Mariniset*. It is possible to recognise the *Multifidus* in the thoracic region, but the *Semi-spinalis* is very weak and can just be recognised as a separate muscle mass in the upper thoracic and lower cervical region.

Muscles of the Tail.

M. Levator Caudæ Externus arises from the transverse process of the fourth and fifth lumbar vertebræ and the adjacent portion of the ilium. The muscle forms a number of tendons which are inserted into all the caudal vertebræ. Each tendon is inserted into a caudal vertebra. The muscle fades out about the third or fourth vertebra.

M. Levator Caudæ Internus is fused above with the *longissimus dorsi*. The origin is very extensive. Fibres are derived from the lombo-dorsal fascia, the transverse processes of the lower ten dorsal vertebræ, and the spines and dorsal surfaces of the lumbar and sacral vertebræ. Some fibres also arise from the upper two or three caudal vertebræ. The muscle becomes tendinous about the fourth caudal vertebra and the tendons are inserted into all the caudal vertebræ.

Mm. Depressores Caudæ or *M. Sacro-coccygeus ventralis* arise from the deep or pelvic surfaces of the last sacral and the upper three caudal vertebræ. Tendons pass into the ventral surface of each caudal vertebra as far as the tip of the tail. The muscle tissue ends over the third or fourth caudal vertebra. Like the *levatores caudæ* these muscles are very slender.

M. Pubo-coccygeus arises from the pubis as far forward as the symphysis and forms a fan-shaped muscle which is inserted into the third caudal vertebra.

M. Ilio-coccygeus arises from the iliac portion of the pelvic brim and the pelvic surface of the body of the ilium. It is inserted into the first, second, and third caudal vertebræ. The main insertion is into the third caudal vertebra.

M. Ischio-coccygeus is the deepest of the three abductor muscles of the tail. It arises from the pelvic surface of the ischium and is inserted into the lateral surfaces of the first two caudal vertebræ.

*The Muscles of the Upper Extremity.**Anterior and Thoracic Region.*

Pectoralis major M.—The pectoralis major is divided into two portions—the sternal and the abdominal. The pars sternalis arises from the whole length of the sternum, the fibres converging to form a fan-shaped mass which is inserted into the humerus. The lower fibres wind round the upper fibres from the manubrium and the upper part of the sternum, and hence the insertion of the muscle presents a flattened U-shaped form. In this way the lowest fibres reach towards the highest level of the insertion. The insertion of the sternal part is along the summit of a well-marked ridge to the medial side of the bicipital groove of the humerus and downwards along the shaft of the humerus in the same plane to the level of the deltoid insertion. The uppermost fibres of the tendon of insertion appear to blend with the capsule of the shoulder-joint. The muscle is supplied by four twigs—two from the lateral anterior thoracic and two which pierce the pectoralis minor.

The pars abdominalis is a thin slip of muscle which arises from the upper five millimetres of the linea alba and from the ninth and tenth costal cartilages at their junction with the sternum. Passing laterally and upwards it lies deep to the sternal portion and is inserted deep to that muscle along the bottom of the pectoral crest. Some fibres are inserted into the capsule of the shoulder-joint. The nerve supply of the pars abdominalis is from the medial anterior thoracic.

Pectoralis minor M.—The muscle arises from the costal cartilages of the second to sixth ribs near the junction of these with the sternum. It is a fan-shaped muscle, the fibres converging to a well-marked tendon which passes upwards and laterally where it blends with the capsule of the shoulder-joint on its superior surface. By this means the muscle obtains attachment to the great tuberosity and the acromion process, and the nerve supply is from the medial anterior thoracic nerve and from one or two communicating branches from the lateral anterior thoracic nerve. In one specimen the branches from the lateral anterior thoracic nerve joined the medial anterior thoracic nerve to form a single trunk.

Subclavius M.—This is a small fusiform muscle which arises from the medial end of the first costal cartilage and is inserted into the deep border of the clavicle near the lateral end of that bone. It is supplied by a nerve which comes off from the 5th and 6th cervical nerves.

Latissimus dorsi M.—This muscle has a very extensive origin from the spines and the interspinous ligaments of the fourth thoracic to the third lumbar vertebræ. In addition, it obtains fibres of origin which arise from the posterior lamella of the lumbo-dorsal fascia, and in this way the origin is carried as far back as the iliac crest. The muscle fibres from the fascial origin

commence about the level of the last rib. These lower fibres wind round in the same manner as the fibres of the lower part of the pectoralis major muscle, and hence the most anterior or the deep fibres at the insertion are those from the lowest part of the origin. At the level of the inferior angle of the scapula the fibres of the dorsi-epitrochlearis pass off in two muscle bundles. In two of the specimens the division into two heads was not seen. The muscle fibres forming the dorsi-epitrochlearis part of the latissimus dorsi arise from the uppermost part of the origin of the muscle. Some fibres of the dorsi-epitrochlearis arise from a tendinous intersection in the lower part of the muscle. The nerve of supply to the muscle is from the Musculo-spiral in the axilla. The nerve runs along the deep aspect of the muscle and supplies it. The main part of the muscle runs along the inferior border of the scapula and is inserted into the humerus along the floor of the bicipital groove. The muscle is pierced by the terminal branches of the posterior divisions of the spinal nerves from the fourth thoracic to the third lumbar segment and by the lateral branches of the fifth to the tenth thoracic nerves.

Muscles of the Shoulder Region.

Deltoid M.—This muscle consists of three parts—a clavicular, spinal, and acromial. The clavicular part arises from the lateral half of the clavicle from the anterior border. Medially its fibres are in relation with the fibres of the pectoralis major but do not fuse with it. The acromial part arises from the acromial process and from the spine of the scapula for about the lateral fourth of its length. The spinal part is separate from the remainder of the muscle and it arises from the remainder of the spine of the scapula from its lower border. The fibres of the former two parts converge on a median raphe which extends from the acromial process to the lowest part of the lateral bicipital ridge. The clavicular fibres are inserted into this raphe along its anterior edge. The acromial fibres converge on it from behind to form a herring-bone pattern. The spinal part is muscular along the whole of its length and does not find any attachment to the raphe. The insertion of the anterior two parts of the deltoid is into the lowest part of the lateral bicipital ridge. The spinal part is inserted a little posterior to the insertion of the former parts. The whole of the muscle is supplied by the axillary nerve.

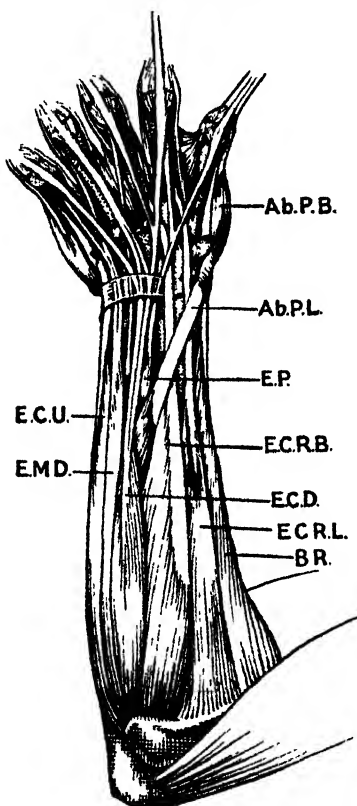
Supraspinatus M.—The muscle arises from the whole of the supra-spinous fossa of the scapula. The fibres converge on a short tendon that is inserted into the great tuberosity of the humerus at its uppermost part.

Infraspinatus M.—The infraspinatus arises from the whole of the infraspinous fossa of the scapula and from the lower surface of the spine. The main part of the muscle arises near the vertebral border. The fibres are inserted into the great tuberosity

of the humerus immediately distal to the insertion of the supraspinatus. The muscle is not split into two parts as in the Lemurs and *Tarsius*.

Teres minor M.—This muscle arises from the lateral half of

Text-figure 27.



The extensor musculature of the forearm and hand.

B.R. Brachio-radialis or supinator longus M. E.C.R.L. Extensor carpi radialis longus M. E.C.R.B. Extensor carpi radialis brevis M. E.C.D. Extensor digitorum communis M. E.M.D. Extensor minimi digiti M. E.C.U. Extensor carpi ulnaris M. Ab.P.L. Abductor pollicis longus M. Ab.P.B. Abductor pollicis brevis M. E.P. Extensor pollicis portion of extensor digitorum communis tendons.

the inferior border of the scapula. It is a thin muscle which is covered almost entirely by the infraspinatus. The fibres are inserted into the great tuberosity of the humerus distal to the insertion of the infraspinatus.

Teres major M.—The fibres arise from the inferior angle of the scapula and from that part of the inferior border which does not give origin to the teres minor. Passing deep to the long head of the triceps and superficial to the tendon of the latissimus dorsi, it finds insertion into the medial border of the bicipital groove. The muscle is a powerful mass of fibres larger than the mass of the infraspinatus.

Subscapularis M.—The fibres of this muscle arising from the subscapular area are divided into four well-marked strands. Converging together the tendinous parts fuse together to form a single tendon of insertion into the lesser tuberosity of the humerus.

Muscles of the Upper Arm.

Triceps M.—The tendon of insertion of the Triceps into the olecranon of the ulna receives fibres from five different sources. In this way the muscle is identical with the condition found in *Tarsius*.

(1) The long head of the triceps arises to the outer side of the glenoid cavity of the shoulder-joint. The fibres take origin from the glenoid lip itself and from the four millimetres of inferior border of the scapula immediately alongside the glenoid lip. This part forms the biggest contribution to the triceps tendon.

(2) The lateral head of the triceps arises by a thin tendon attached to the great tuberosity of the humerus distal to the insertion of the teres minor. The fibres converge on the fibrous lateral edge of the long head and are inserted into it and into the olecranon.

(3) The medial head of the triceps arises from the shaft of the humerus distal to the capsule of the shoulder-joint in the plane between the insertion of the teres minor and the insertion of the teres major. The fibres run distally to the olecranon and obtain fibres from the posterior aspect of the shaft of the humerus along the upper half.

(4) The anconeus arises from the distal half of the shaft of the humerus in the same plane as the medial head. It is quite distinct from the medial head of the triceps and is inserted directly into the olecranon and into the lateral part of the main tendon.

(5) The dorso-epitrochlearis arises from the lower margin of the latissimus dorsi before it passes deep to the long head of the triceps. The nerve supplying this part of the triceps is from the nerve to the latissimus dorsi.

Biceps M.—Long head arises from the upper margin of the lip of the glenoid fossa of the scapula. The tendon is embedded in the capsule of the shoulder-joint deep to the fibrous capsule. The tunnel in which it passes downwards is attached to the lips of the bicipital groove of the humerus which is well marked. The short head is a very thin strip of muscle and tendon which

arises in common with the superficial part of the coracobrachialis from the coracoid process of the scapula. The short head joins with the long head about the level of the deltoid insertion. The fibres blend and form a common mass which passes into the forearm and finds insertion into the bicipital tubercle of the radius. The tendon is narrow and the muscle fibres do not end until very close to the insertion. There is no reinforcement of the deep fascia of the antecubital fossa from the tendon of the muscle.

Coraco-brachialis M.—The origin of this muscle arises in two parts from the coracoid process of the scapula. The superficial part arises from the tip of the process in common with the tendon of origin of the short head of the biceps. This portion is inserted into the medial epicondylar ridge of the humerus. The deep part arises from the coracoid deep to the superficial portion and passes into the shaft of the humerus just distal to the head, above the level of the insertion of the latissimus dorsi. The musculo-spiral nerve passes between the two parts.

Brachialis anticus M.—Arising from the shaft of the humerus immediately distal to the insertion of the deltoid and from the anterior edge of the lateral epicondylar ridge, the fibres pass distally into the forearm to be inserted into the coronoid process of the ulna. The upper part of the origin passes above the deltoid insertion on the outer side of the shaft and so forms the lateral boundary of the musculo-spiral groove.

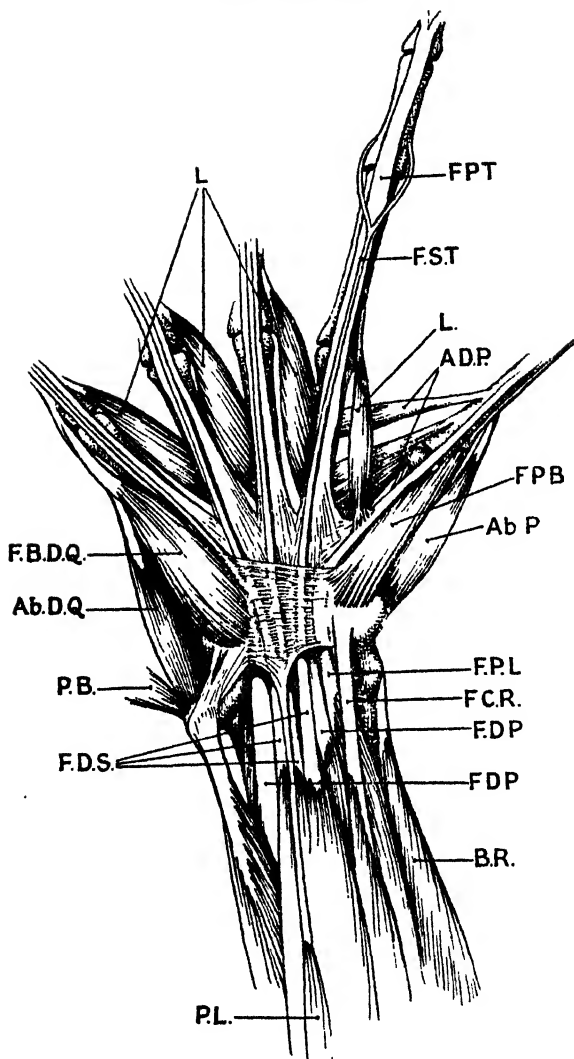
Extensor Musculature of the Forearm.

Supinator longus M.—The origin of this muscle is from the highest part of the lateral epicondylar ridge of the humerus. The fibres pass downwards into the forearm and are inserted by means of a very thin tendon into the radius at the base of the styloid process.

Extensor carpi radialis longus M.—The fibres of origin of this muscle arise slightly lower down the lateral epicondylar ridge of the humerus. The origin is common to both the supinator longus and the extensor carpi radialis longus, and it is almost impossible to separate the two masses from each other at the origin. The muscle is tendinous throughout the lower half of its course. At the base of the styloid process of the radius the tendon lies deep to the tendon of insertion of the abductor pollicis longus. This tendon crosses from the ulnar side to the radial side of the forearm to reach the pollex. The insertion of the muscle is into the base of the first metacarpal bone. In this it differs from the condition found in *Tarsius*.

Extensor carpi radialis brevis M.—Like the previous two muscles this mass arises from the lateral epicondylar ridge of the humerus. The tendon passes deep to the abductor pollicis longus and the extensor pollicis longus. The insertion is into the base of the second metacarpal.

Text-figure 28.



Flexor muscles of the forearm and hand.

F.D.S. Flexor sublimis digitorum M. F.D.P. Flexor digitorum profundus M. F.P.T. Flexor profundus tendon. F.S.T. Flexor sublimis tendon. L. Lumbrical Mm. Ad.P. Adductor pollicis M. Transverse and oblique parts were present in this specimen. F.P.B. Flexor pollicis brevis M. F.P.L. Flexor pollicis longus M. Ab.P. Abductor pollicis M. F.C.R. Flexor carpi radialis M. B.R. Supinator longus M. P.L. Palmaris longus M. P.B. Palmaris brevis M. Ab.D.Q. Abductor digiti quinti M. F.B.D.Q. Flexor brevis digiti quinti M.

Extensor digitorum communis M.—The muscle arises from the lateral epicondyle of the humerus. The muscle is a very weak mass, the muscle fibres being replaced by tendon about the mid-point of the forearm. The small tendon passes deep to the dorsal annular ligament and over the carpus it splits into five thin slips to each of the five digits. The insertions are into the dorsal surfaces of the bases of the terminal phalanges where the tendons come into intimate relation with the base of the claws. As the tendons pass over the inter-phalangeal joints the fibres expand and some are inserted into the lateral ligaments of the joint capsules.

Extensor minimi digiti M.—This muscle arises to the ulnar side of the common extensor of the fingers as a thin mass of fibres. At about the same point as the common extensor the tendon of insertion appears. There are muscular fibres on the deep surface of the mass as far distal as the dorsal annular ligament. After passing under the ligament the tendon divides into two parts. The division is apparent for about five or six millimetres before the tendon passes under the annular ligament. The two tendons diverge, one in a radial and one in an ulnar direction. The ulnar tendon lies considerably to the ulnar side of the slip of tendon of the common extensor going to the fifth digit. The two fibres unite over the first interphalangeal joint. The radial slip passes deep to the slip of the common extensor to the fifth digit and passes along the ulnar side of the fourth digit joining the common extensor tendon (long) over the first interphalangeal joint.

Extensor carpi ulnaris M.—The fibres arise from the lateral epicondyle of the humerus, from the ulnar side of the olecranon process, and the ligamentous structures between these two bones. They form a well-defined fleshy mass which becomes tendinous on the outside half-way to the annular ligament. The tendon is fully formed as it passes under the ligament. The tendon lies in a separate compartment on the ulnar side of the long extensor tendon and the extensor minimi digiti. The insertion is into the base of the fifth metacarpal.

Abductor longus pollicis M.—The fibres arise from the upper two-thirds of the dorsal surface of the radius from the interosseous membrane along its proximal half and from the upper part of the shaft of the ulna close to the insertion of the interosseous membrane. The muscle lies on the dorsal surface of the radius and crosses superficial to the radial carpal extensors. The tendon is inserted into the radial surface of the base of the first metacarpal bone. The tendon lies in a tunnel formed between the dorsal carpal ligament and the radial margin of the carpus.

Extensor longus pollicis M.—This muscle is entirely wanting in the specimens dissected.

Extensor indicis M.—The muscle arises from the ulna along the upper two-thirds of its dorsal border. The muscle is a very

thin slip, and a tendon appears on its dorsal aspect about the mid-point of the ulna. This tendon separates off to the radial side, and the remainder of the muscle forms another tendon on the ulnar side. The former tendon passes in the deepest part of the tunnel beneath the dorsal annular ligament, and over the middle of the shaft of the second metacarpal it splits into two slips, a radial going to the first digit and forming the long extensor of that digit. The remainder of the tendon passes on, lying on a deeper plane than the common extensor tendons and fuses with the extensor tendon to the second digit over the first interphalangeal joint. The tendon formed on the ulnar side of the muscle in the forearm lies on a deeper plane than the radial tendon in the carpal tunnel. It passes into the third digit and fuses with its long extensor tendon in the same way as the radial part of the muscle. A very thin slip passes to the long extensor tendon of the fourth digit. The connection was not true tendon but was, as Woollard found in *Tursius*, a fascial connection. There is no radial origin in any of the five specimens dissected.

Flexor Musculature of the Forearm.

Pronator radii teres M.—The fibres arise from the medial epicondyle of the humerus towards the deeper aspect of the process. The fibres, which are never more than two centimetres long, sweep outwards to the radius and are inserted over the middle third of the shaft of the bone. The median nerve lies deep to the muscle.

Flexor carpi radialis M.—The muscle arises more from the medial side of the common flexor origin than the pronator radii teres. The muscle fibres end about half-way along the forearm in a tendon. The tendon passes in the tunnel beneath the transverse carpal ligament and is inserted into the base of the second metacarpal.

Palmaris longus M.—The muscle fibres composing this muscle cannot be defined from the main flexor mass arising from the medial epicondyle until just a few millimetres from the origin of the tendon of insertion of the muscle. The tendon, which is a very thin structure, passes downwards over the transverse carpal ligament, where it becomes flattened out into a thin sheet of fascia which covers the whole of the palm. This sheet is very thin and has attached to it the fatty and fibrous tissue composing the pads of the palmar surface of the hand.

Flexor carpi ulnaris M.—Arising from the common origin of the flexors the muscle obtains fibres also from the posterior part of the elbow-joint, the medial edge of the olecranon, and the shaft of the ulna along its medial border for the upper two-thirds of the length of the shaft. Fibres are also arising from the deep fascia of the forearm. The tendon does not appear until the muscle reaches the distal third of the forearm when it separates as a thick mass to be attached to the fifth metacarpal *via* the pisiform bone.

Flexor sublimis digitorum M.—This very thin mass of muscle fibres arises by a narrow thin tendon from the median epicondyle of the humerus. In the distal third of the arm the muscle breaks up into four tendons which proceed to the medial four digits. Over the metacarpo-phalangeal joints the tendons lie in a gutter formed by the division of the profundus tendon. They split into two about the middle of the shaft of the proximal phalanx and, continuing alongside the profundus tendon, they unite below it at the first interphalangeal joint and are inserted along the distal margin of the capsule of the joint into the base of the second phalanx. The muscle is extremely thin and the insertions are very weak. It is possible that a number of the fibres are attached to the lateral ligaments of the first interphalangeal joint.

Flexor profundus digitorum M.—There is no connection between this muscle and the sublimis. The muscle is easily three times greater in bulk than the sublimis. The origin is very extensive fibres arising from the medial epicondyle of the humerus, the medial surface of the ulna in its upper half, the interosseous membrane, and the upper two-thirds of the shaft of the radius on its anterior surface. It is impossible to make a real separation between the profundus and the flexor pollicis longus. They are bound together much more closely than in *Tarsius*. There is no common tendon formed which afterwards breaks up into the slips to the various digits. On the contrary, the muscle is split up from its origin into six well-marked tendons. These tendons are connected to each other by tendinous slips while in the carpal tunnel (text-figure 28).

Leaving aside the flexor pollicis longus portion, the tendons of the profundus when they enter the carpal tunnel give off connecting tendons which unite the several tendons with their fellows on each side. The most lateral tendon receives a connection from the pollicis longus, and the most medial tendon gives off a connection to its fellow on the lateral side. From this tendinous plexus four tendons arise which pass into the medial digits. The tendons are bound down over the metacarpo-phalangeal joints and over the interphalangeal joints lying in a tunnel in the capsule of the joint cavity. The relation of the sublimis tendon is described above. The tendons continue distally and are inserted into the terminal phalanges on the ventral or palmar surface. The terminal pads are firmly attached to the tendons at their insertions.

Flexor pollicis longus M.—The fibres of origin of this muscle form the most lateral part of the origin of the profundus mass. They arise entirely from the radial shaft and by a thin tendon from the medial epicondyle of the humerus. At the entrance to the carpal tunnel it gives off a slip from the tendon to the tendon of the most lateral of the profundus tendons. On leaving the tunnel it gives off another slip to the tendon to the index finger. There is no fusion of the tendons of the longus pollicis

and the lateral tendon of the profundus. The insertion of the tendon is into the base of the terminal phalanx of the pollex.

Pronator quadratus M.—This is a small muscle which extends for less than one fourth of the length of the radius and ulna. The ulnar origin extends upwards as far as the upper limit of the distal third of the forearm, and sloping across to the radius it is inserted into that bone over a small area of the palmar surface of the radius and the lateral border of the bone. The volar interosseous nerve passes deep to the muscle fibres and lies on the interosseous membrane.

Muscles of the Hand.

Palmaris brevis M.—This is represented by a few muscular fibres which lie deep to the skin of the hypothenar eminence. It is covering the whole of the area of the hypothenar pads. The fibres arise from the medial side of the transverse carpal ligament and are inserted into the fascia over the head of the metacarpal bone.

Lumbricals.—The lumbrical muscles are four in number and are very well developed. They arise from the radial side of the profundus tendons to the lateral three digits. There is no origin from the flexor pollicis longus muscle. The lumbrical muscle to the fifth digit arises from the ulnar side of the tendon to the fourth digit. They all pass to the lateral side of the profundus tendons and are inserted into the base of the proximal phalanx and into the dorsal expansion of the metacarpophalangeal joints.

Abductor pollicis brevis M.—This is a very thin mass of muscle. It arises from the trapezium and the transverse carpal ligament at its radial side. The fibres pass upwards on the radial side of the metacarpal and are inserted into the base of the first phalanx.

Adductor pollicis M.—This muscle is present in *Hapale*.

Flexor brevis pollicis M.—The flexor brevis pollicis arises mainly from the trapezium. A few fibres arise from the radial edge of the transverse carpal ligament along with the fibres of the abductor pollicis. The fibres are inserted into the radial and ulnar sides of the base of the first phalanx. They form a very strong short flexor.

Opponens pollicis M.—This muscle is absent in all the specimens dissected.

Abductor minimi digiti M.—Arises from the ulnar edge of the transverse carpal ligament, the superficial surface of the pisiform, and from the carpal surface of the unciform bone. It is inserted into the dorsal extensor expansion over the metacarpophalangeal joint and into the ulnar side of the base of the first phalanx.

Flexor brevis minimi digiti M.—This small muscle arises from the unciform and is inserted into the base of the first phalanx. It is quite separate from the abductor minimi digiti.

Opponens minimi digiti M.—This muscle is absent in *Hapale*.

Palmar interossei Mm.—The palmar interossei and the dorsal interossei form a continuous mass of muscle fibres on the carpal surfaces of the metacarpal bones. There are eight muscles. Two muscles are present for each interdigital cleft. The fibres run upwards along the metacarpal bones and become attached to the lateral parts of the capsules of the metacarpo-phalangeal joints. There is no continuation upwards of the tendons or insertion as takes place in *Tarsius*. In this respect the interossei, although arising as in *Tarsius*, have a different insertion and different function.

The Muscles of the Lower Extremity.

Anterior Femoral Region.

Sartorius M. arises from the anterior superior spine of the ilium. It is a thin strap-like muscle which expands as it nears its insertion along the medial surface of the upper part of the tibia. It lies superficial to the insertion of the gracilis and semitendinosus tendons. It is supplied by the femoral nerve. Jamieson (1904) describes the insertion as much more limited than the above description and states that the muscle has the same width throughout all its course. Some of the muscle fibres arise from the ventral edge of the ilium, being thus intermediate between the condition in the Lemurs, where the whole origin is along this region, and the condition in the higher monkeys, where the origin is confined to a very small area of the ventral edge of the ilium.

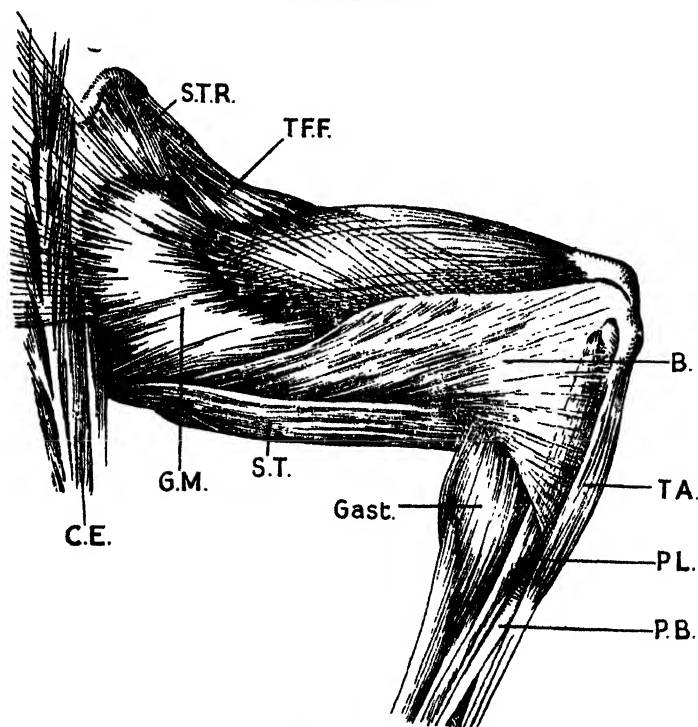
Rectus femoris M. has two heads of origin: (a) a straight head from the anterior inferior iliac spine and a small area of bone lateral to it, and (b) a reflected head from the bone immediately above the acetabulum. Jamieson has described a long tendon embedded within the substance of the rectus, which is continuous with the reflected head. I have found this tendon to be present only in three cases out of six dissected. When present it has the relations he describes. The muscle is inserted into the upper edge of the patella by tendinous fibres, very few muscle fibres reaching the bone. The anterior tendinous fibres are continued superficial to the patella to reach the ligamentum patellæ and thus are inserted into the tibial tubercle.

Vastus lateralis M. arises from the lower part of the great trochanter of the femur and from the upper half of the outer or lateral surface of the shaft of the femur. The fibres form a large mass which converges on a tendinous sheet to be inserted into the lateral aspect of the patella. The vastus does not obtain any fibres of origin from the linea aspera.

Vastus medialis M. has a small origin from the inner half of the anterior intertrochanteric line and from the femur immediately below this. The origin is a small area compared with that in the higher primates. The fibres form a fusiform mass which

converges on the inner border of the patella. The vasti as they approach the patella give off fibrous expansions which, on the lateral side, is attached to the lateral aspect of the capsule of the knee-joint and also with the fascia covering the lateral aspect of the leg. The expansion from the vastus internus is inserted

Text-figure 29.



The superficial muscles of the lateral thigh region.

S.T.R. Sartorius M. T.F.F. Tensor fasciae femoris M. B. Biceps M. T.A. Tibialis anticus M. P.L. Peroneus longus M. P.B. Peroneus brevis M. Gast. Lateral head of gastrocnemius M. S.T. Semitendinosus M. G.M. Gluteus maximus M. C.E. Extensor muscles of the tail.

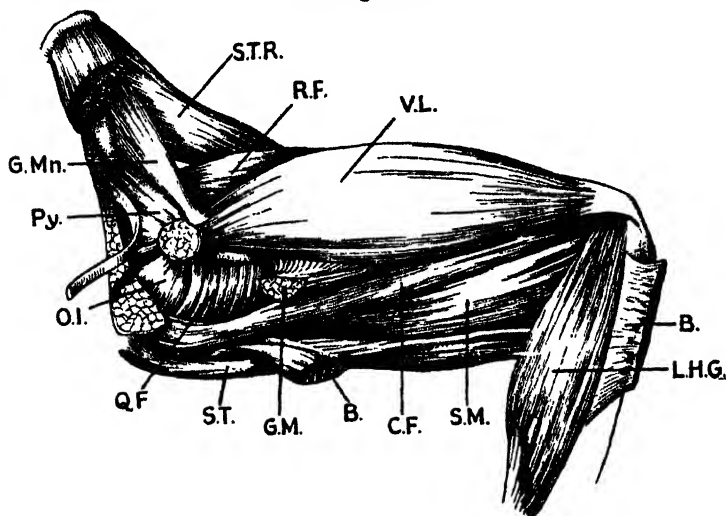
similarly. It reaches to the internal lateral ligament and is continued down to be attached to the upper margin of the insertion of the sartorius.

The main tendons of the vasti send their superficial fibres deep to the rectus tendon and superficial to the crureus. These fibres reach the upper border of the patella into which they are inserted.

Crureus M. arises from the upper three-fourths of the shaft of

the femur. The upper fibres lie between the origins of the vasti muscles. It is a rather thin muscle, and as it passes down the shaft, fibres converge on it from the lateral and medial surfaces of the femur. Jamieson has described, on the deep surface of the blended tendons of the vasti, a small piece of cartilage into the superficial aspect of which the blended vasti tendons are inserted and into whose deep surface the crureus is attached. This condition was found to be constant in almost all the specimens examined. In two animals the cartilage had fused with the patella and had become ossified.

Text-figure 30.



The deep muscles of the lateral thigh region.

G.M. Gluteus maximus M. G.Mn. Gluteus minimus M. R.F. Rectus femoris M. S.T.R. Sartorius M. V.L. Vastus lateralis M. B. Biceps M. L.H.G. Lateral head of gastrocnemius M. S.M. Semi-membranosus M. S.T. Semitendinosus M. Q.F. Quadratus femoris M. O.I. Obturator internus and gemelli muscles. Py. Piriformis M. C.F. Caudo-femoralis M.

The main mass of the fibres of the crureus are inserted into the cartilage or its ossified representative, but some of the deep fibres are attached to the synovial membrane, which forms a pouch passing superior to the patella. These fibres, as Jamieson has noted, could not be separated off from the main mass of the crureus.

The quadriceps is supplied by fibres from the anterior crural or femoral nerve. The Lemurine condition, as shown by Murie and Mivart in *Galago* (1872), is identical with the condition in *Hapale*.

The Adductor Group of Muscles.

Dr. A. B. Appleton, of Cambridge University, has supplied me with his conclusions based on the dissection of several specimens of *Hapale*. I am deeply indebted to him for this information, which has confirmed the observations which I have made on this region.

He states:—"The adductor musculature consists of

- (a) Adductor magnus.
- (b) Adductor brevis.
- (c) An inconstant Adductor longus and
- (d) a series of accessory adductor muscles.

The accessory adductor muscles are attached proximally to the Art. perforans prima. Two of them are attached in common with the pectineus to a groove proximal to the nutrient branch from the Art. perforans prima. The third accessory adductor muscle is attached more laterally. The attachment of these muscles confers on them a lateral rotary action (on the femur relative to the pelvis).

The distal part of the adductor magnus proper is attached to the femur between the caudo-femoralis and the præ-semimembranosus. A slight groove marks the site of the attachment of its middle part. The site of the attachment of the mm. adductores brevis and longus is marked by a groove. The femoro-coccygeus is attached to a septal line (lateral) extending distally from the third trochanter as far as the insertion of the caudo-femoralis and lateral to it. The quadratus femoris has a restricted attachment to the margin of the quadrate fossa about the level of the lesser trochanter. The medial circumflex artery passes between the quadratus femoris and the ilio-psoas on the one hand and the pectineus and the adductor musculature on the other.

The nerve to the gracilis m. separates the adductores into two groups; it passes between

- (a) the adductor longus, pectineus and the first accessory adductor and
- (b) the other adductor muscles.

The nerve to the gracilis is associated with the nerves which with it make up the dorsal division of the obturator nerve. The muscles supplied by this division of the obturator nerve are all the adductors with the exception of the adductor magnus and the third accessory adductor muscle.

The thigh and buttock of *Hapale jacchus* presents a structural pattern of a primitive Eutherian type. In the retention of a m. tenuissimus and the incomplete differentiation of the gluteus maximus and the femoro-coccygeus it presents features found in many Primates as well as in various other Eutheria. But in the retention of a dorsal head to the hamstring musculature (here represented by a caudal head of the semitendinosus) it presents a

primitive feature not yet observed in any other Primate or Prosimian, though it is found in *Tupaia ferr.* and in the more primitive members of various mammalian orders. There is also a caudo-femoralis with caudal origin as in *Tupaia* (but unlike *Macroscelides*). This muscle is retained in various Prosimiæ, but has not yet been observed in other Primates.

Some differentiation of proximally-inserted accessory adductor muscles has occurred, with attachments conferring on them a lateral rotator effect on the thigh. The peculiar distal extension of the insertion of the quadratus femoris found in some Prosimiæ has not occurred in *Hapale*.

The thigh of *Hapale* presents in the arrangements of muscles, nerves, and arteries a very close resemblance to the thigh structure of *Tupaia ferr.*, differing mainly in the differentiation of the series of accessory adductor muscles. Both *Macroscelides* and *Tarsius* present considerable modifications of the primitive pattern seen in *Hapale*."

Posterior Femoral Region.

Tensor fasciæ femoris M. has been described by Jamieson as being divided into two parts, an inferior and a superior. This division is, I think, entirely artificial, as I have specimens which show all the stages between two distinct muscles and a single muscle mass. In *Hapale* the muscle is quite independent of the gluteus maximus m. It arises from the ilium along its border below the anterior superior spine and from the fascia which covers the gluteus medius, as far back as the posterior superior iliac spine. The fibres converge rapidly and are inserted into the fascia lata of the thigh in the region distal to the great trochanter. Anteriorly the fibres may blend or may be separate from the inferior part described by Jamieson. This latter part arises from the region of the anterior inferior spine lateral to the process itself. The fibres lie deep to the fibres from the upper part of the ilium and are inserted into the fascia lata slightly distal to the insertion of the upper fibres.

The nerve-supply is from the superior gluteal nerve. Macalister has described as an anomaly in Man the division of the tensor into two parts, a superficial and a deep. This would parallel the condition found in some specimens of *Hapale*.

Gluteus maximus M. consists of two portions closely united. The two parts are only separable at their origins—the superficial or more cephalic head arises from the lumbar fascia, which lies superficial to the erector spinæ mass of muscle in the vertebral groove, and the deep, which arises from the caudal vertebræ ventral to this erector mass. The superficial portion is thin, and as it passes into the thigh the deeper fibres converge on a thin tendon which is inserted into the base of the great trochanter on its lateral aspect. The superficial fibres are inserted into the femur in common with the deep part of the muscle. This latter

part arises from the lateral surface of the caudal vertebræ by two distinct heads of origin. One lies superficial to the ilio-coccygeal and supra-caudal muscles and the other deep to this mass. The two parts unite and are inserted into the femur along its posterior aspect for the upper two-thirds of the shaft. Between the hamstrings and the gluteus maximus there is a strong inter-muscular septum which is given off from the fascia lata and which is attached to the posterior surface of the femur. Into this septum a number of the fibres of the superficial part of the muscle are inserted. Jamieson describes a considerable amount of muscle as being inserted into the fascia lata in common with the tensor fascia femoris. I did not find this as extensive as he has described.

The nerve-supply of the muscle is from two distinct nerves from the great sciatic. One branch goes to the superficial and one to the deep portion of the muscle.

Gluteus medius M. arises from the dorsal part of the lateral surface of the wing of the ilium, from the posterior fibres of the sacro-iliac joint, and from the dorso-lateral part of the first caudal vertebra. The muscle is large and converges on the upper part of the great trochanter, into which it is inserted as well as into a small area on the posterior surface. The muscle is supplied by the superior gluteal nerve.

Gluteus minimus M.—The gluteus minimus varies considerably in the formation of its several bundles. Jamieson has described four separate masses of muscle as entering into the composition of the muscle. It is most constant to find a separate anterior portion which would correspond to a scansorius, but the three other divisions are never quite so distinct as has been described by the above author. The origin of the muscle was from the dorsum of the ilium over the posterior half of this surface. The fibres converge on the great trochanter and are inserted into its anterior and upper surface.

Scansorius M.—This muscle is in reality a portion of the gluteus minimus in the animals I have dissected. It is the most anterior part of the gluteus minimus and has a separate existence, until just before it is inserted into the trochanter. It develops a thin tendon which passes superficial to all the other parts of the gluteus minimus and is inserted into the lateral aspect of the great trochanter. The nerve-supply to the minimus and to the scansorius is from the superior gluteal nerve.

Gemellus superior M. arises from the region of the small ischial spine and is inserted into the obturator internus tendon.

Gemellus inferior M. is almost twice the size of the superior. It arises from the ischial tuberosity and is inserted into the obturator internus tendon. The superior is supplied by a small nerve from the great sciatic nerve, and the inferior receives its nerve-supply from the nerve to the quadratus femoris.

Obturator internus M. arises from the obturator membrane and from the bones surrounding the obturator foramen. The muscle

obtains fibres from the bone as high as the upper limit of the superior ramus. The tendon passes out of the pelvis over the ischium in the lesser sciatic notch which is relatively poorly marked. The tendon on reaching the thigh is covered over by the gemelli except near the insertion, which is on the medial side of the great trochanter in a small depression at the base of the trochanter. It is supplied by the great sciatic nerve through a small branch which is sometimes united with the internal pudendal nerve.

Obturator externus M. arises from the femoral aspect of the obturator membrane and from the bone on the medial, upper, and lower margins of the obturator foramen. The tendon is thick and lies in relation to the neck of the femur and is inserted into the neck near the insertion of the tendon of the obturator internus. The actual insertion is into the base of the digital fossa. The muscle is supplied by the obturator nerve.

Piriformis M.—This muscle is quite distinct in *Hapale*. It arises from the three pieces of the sacrum along the line of the anterior sacral foramina. The fibres converge on a small tendon which is inserted into the upper limit of the great trochanter. It is supplied by a nerve direct from the plexus which comes from the last lumbar nerve. The first sacral sends a small branch to the nerve in some cases.

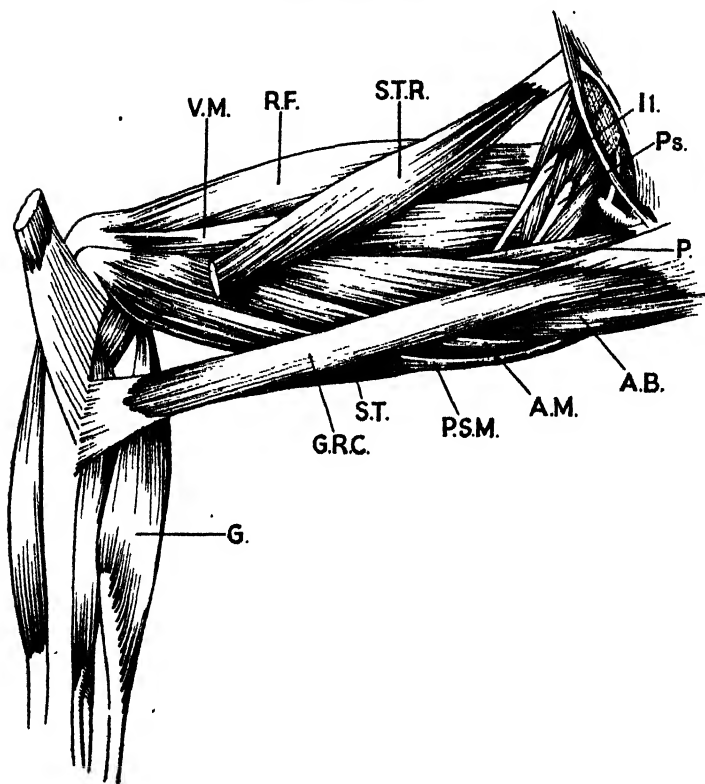
Caudo-femoralis M.—The caudo-femoralis arises from the first and sometimes also derives fibres from the second caudal vertebra. The muscle is close to the origin of the semi-tendinosus from the caudal vertebrae. It lies deep to the origin of the gluteus maximus from this region. It is separated off from this muscle by the great sciatic nerve. The insertion is into the posterior surface of the femur in its middle third. The fibres of insertion are in close relation to the insertion of the gluteus maximus. Some of the fibres are inserted into the intermuscular septum between the hamstrings and the gluteus maximus. I have only found a single nerve-supply from the nerve to the hamstrings from the great sciatic, and have not observed the connection from the nerve to the gemellus inferior described by Jamieson. I agree with Jamieson that the muscle arose close to the origin of the semi-tendinosus and not in conjunction with the origin of this muscle as described by Windle (1886).

Iliacus M. arises from the internal surface of the ilium. In this region it is almost covered by the large belly of the psoas. It is in relation above with the origin of the quadratus lumborum from the ilium. The muscle passes under the inguinal ligament lateral to the psoas magnus, and in the region of the lesser trochanter it is inserted into the psoas magnus and into the lesser trochanter and a small area of the femoral shaft immediately distal to it. The nerve-supply is derived from the femoral nerve.

Psoas magnus M. arises from the anterior aspects of the bodies of the second, third, fourth, fifth, and sixth lumbar vertebrae and

from the intervertebral discs. Sometimes the slip from the second lumbar is absent, and then it is usual to find a small slip from the first sacral. The muscle lies close to the bodies of the vertebræ and passing under the inguinal ligament is inserted into the lesser trochanter. It is supplied by the third and fourth

Text-figure 31.



The muscles of the medial side of the thigh.

V.M. Vastus medialis M. R.F. Rectus femoris M. S.T.R. Sartorius M. I.I. Iliacus M. Ps. Psoas major M. P. Pectineus M. A.B. Adductor brevis M. A.M. Adductor magnus M. P.S.M. Pre-semimembranosus M. S.T. Semitendinosus M. G.R.C. Gracilis M. G. Medial head of gastrocnemius M.

lumbar nerves and sometimes also receives a branch from the femoral.

Psoas parvus M. lies on the abdominal aspect of the above muscle. It is closely blended with the psoas magnus at its origin, but separates off from the psoas magnus and forms a thin tendon. The muscle arises from the second and third lumbar vertebræ.

The tendon extends throughout two-thirds of the length of the muscle and is inserted into the superior ramus of the os innominatum medial to the point where the psoas magnus crosses that structure. There was no fascial insertion.

Quadratus lumborum M. arises from the posterior part of the iliac crest and also from an area of the abdominal surface of the ala of the ilium. It passes upwards as a thin quadrilateral muscle and is inserted into the lower edge of the last rib and also sends fibres to the transverse processes of the lumbar vertebræ. It is supplied by branches from the last thoracic nerve and from the upper three lumbar nerves.

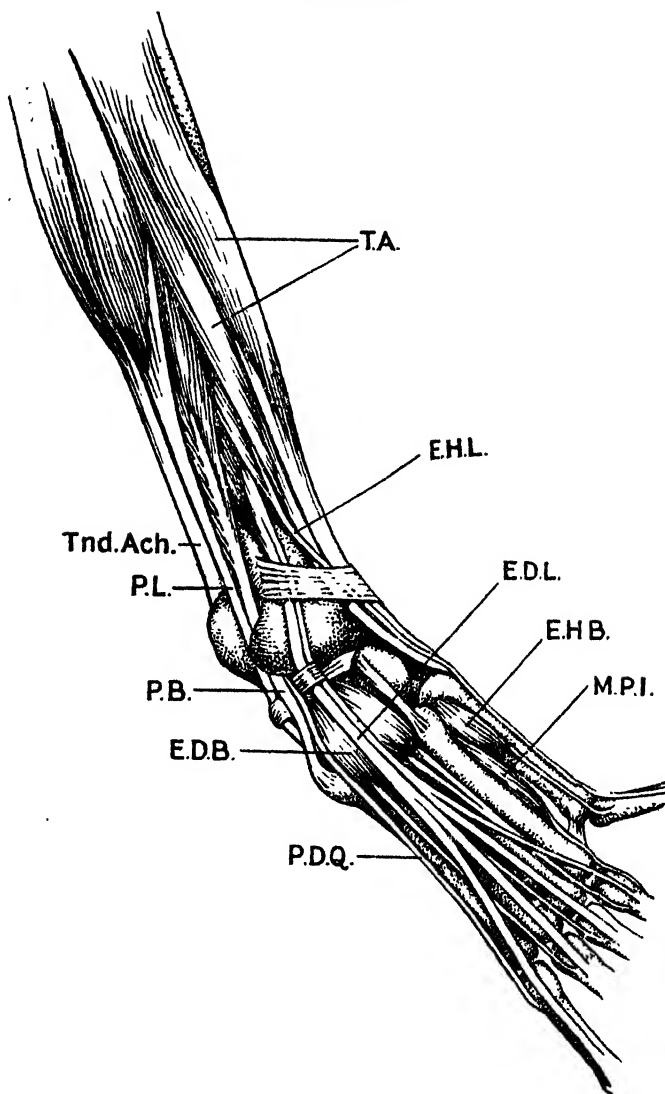
Flexor Region.

Biceps femoris M.—The muscle arises from the posterior aspect of the ischial tuberosity in conjunction with the semi-tendinosus. These two muscles are separated by a strong tendinous band from which they both derive muscle fibres. This tendon is attached to the ischial tuberosity. The muscle fibres form a large belly which later spreads out into a sheet of muscle. This in turn gives rise to a thin aponeurotic expansion which is inserted into the deep fascia of the upper part of the leg, the head of the fibula, the upper part of the lateral condyle of the tibia, and some fibres are seen to pass into the antero-lateral part of the capsule of the knee-joint. The insertion into the capsule is not constant. The fibres which are attached to the head of the fibula are not many, but they constitute a considerable insertion. The muscle is supplied by the nerve to the hamstrings from the great sciatic nerve. There is no trace of a short head.

Semi-membranosus M.—The pre-semimembranosus has been described with the adductor magnus. The semi-membranosus proper arises from the ischial tuberosity close to the origin of the semi-tendinosus. The muscle is inserted into the medial surface of the medial condyle of the tibia. The tendon of insertion gains this position by passing deep to the internal lateral ligament of the knee-joint. From the tendon, fibres are given off to the ligament, and some course deep to the tendon of origin of the medial head of the gastrocnemius to reach the posterior ligament of the knee-joint. The relations of the tendon are discussed more fully in the section on the knee-joint. The pre-semimembranosus can be separated off from the semi-membranosus proper throughout the whole of the course of the muscle.

Semi-tendinosus M.—This muscle arises in common with the biceps from the ischial tuberosity and also by a second head of origin from the first caudal vertebræ close to the origin of the caudo-femoralis. The two blend rapidly after the fibres leave the ischium, and form a thick mass of muscle. The tendon lies superficial to the semi-membranosus in the region of the knee-joint, and gains the medial surface of the shaft of the tibia deep to the gracilis and the sartorius. The tendon is often fused with the tendon of insertion of the gracilis.

Text-figure 32.



The muscles of the anterior region of the leg and of the dorsum of the foot.

T.A. Tibialis anticus M. E.H.L. Extensor hallucis longus M. E.D.L. Extensor digitorum longus M. E.H.B. Extensor hallucis brevis M. M.P.I. Medial plantar interosseus M. P.D.Q. Peroneus digiti quinti M. E.D.B. Extensor digitorum brevis M. P.B. Peroneus brevis M. P.L. Peroneus longus M. Tnd.Ach. Tendo achilles.

Tibio-fibular Region (Extensor Group).

Tibialis Anticus M.—The muscle arises from the lower margin of the lateral condyle of the tibia and from the upper two-thirds of the shaft. The tendon passes under the dorsal annular ligament, where it is seen to expand slightly and to split into two slips. The medial tendon is inserted into the medial surface of the medial cuneiform bone, and the lateral tendon into the head of the first metatarsal.

Extensor Hallucis Longus M.—This is a very thin slip of muscle which obtains its origin from the interosseous membrane about its middle third. It lies deep to the tibialis anticus. The tendon appears before passing under the dorsal annular ligament, where it lies lateral to the tibialis anticus. It is inserted into the terminal phalanx of the hallux. The tendon is bound down to the tarsus and to the head of the first phalanx by definite bands of deep fascia, through which the tendon glides.

Extensor Digitorum Longus M.—The fibres arise from the lower margin of the lateral condyle of the tibia, from the interosseous membrane, and the whole length of the interosseous border of the fibula. Two muscular bellies are formed which give origin to two tendons, one superficial and the other deep. The deep tendon comes to lie on the inner side of the superficial tendon as they both pass beneath the dorsal annular ligament. Over the proximal parts of the shafts of the metatarsals the tendons become bound together, and give rise to four slips which are inserted into the bases of the terminal phalanges of the second, third, fourth, and fifth digits. Over the tarsal region they are bound down in the same way as the tendon of the extensor hallucis.

Peroneus Longus M.—The muscle arises from the head of the fibula, from the fibrous septum between the extensors and the peronei groups, and from the lateral surface of the fibula along the upper half of the shaft. The tendon passes downwards behind the lateral malleolus.

Peroneus Brevis M.—This muscle arises from the lateral surface of the shaft of the fibula over its lower two-thirds. The fibres form a strong tendon which passes behind the lateral malleolus and is inserted into the base of the fifth metatarsal.

Peroneus Quarti Digiti M.—This muscle is absent.

Peroneus Quinti Digiti M.—This small muscle arises from the upper half of the posterior edge of the lateral surface of the fibula deep to the peroneus longus. The tendon lies close to the tendon of the peroneus brevis along its inner border, and is inserted into the dorsal extensor expansion of the fifth digit.

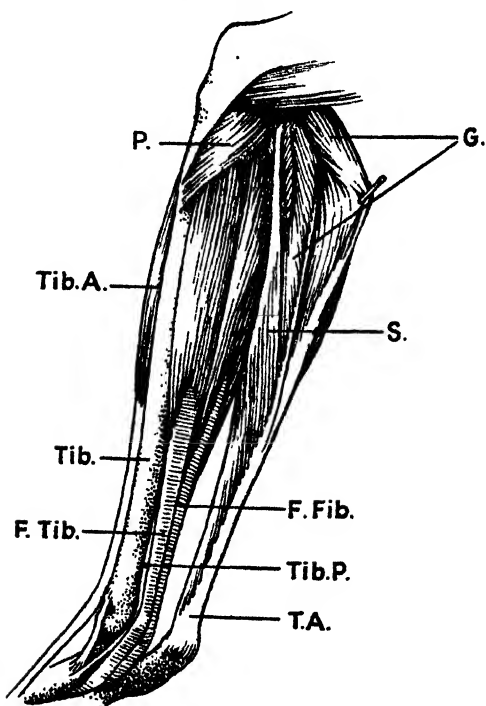
Peroneus Tertius M.—This muscle is absent in *Hapale*.

In passing behind the lateral malleolus the tendons are bound down to the os calcis by strong bands of fascia which are in turn covered by a ligament passing from the tip of the lateral malleolus to the lateral surface of the os calcis.

Tibio-fibular Region (Flexor Group).

M. Gastrocnemius has two heads of origin—a medial head from the upper and posterior part of the medial condyle of the femur, and a lateral from the corresponding area on the lateral condyle. The origins are tendinous until they pass over the posterior aspect of the knee-joint. In each tendon there is a sesamoid bone which articulates with the posterior articular area of the

Text-figure 33.



The flexor region of the leg.

F.Tib. Flexor dig. long. tibialis. F.Fib. Flexor dig. long. fibularis. G. Gastrocnemius M. P. Popliteus. S. Soleus. Tib.A. Tibialis anterior. Tib.P. Tibialis posterior. T.A. Tendo achilles. Tib. Tibia.

lower end of the femur. The muscle fibres form the main mass of the flexor group. In the middle of the leg the tendo Achilles appears, and the muscle fibres become inserted into its lateral side. The tendon is inserted into the upper edge and the posterior surface of the os calcis.

M. Soleus is a thin mass of muscle which arises from the

posterior surface of the head of the fibula. The origin is tendinous and the muscle fibres only appear in a few millimetres before it fuses with the gastrocnemius.

M. Plantaris is relatively thin. It arises from the lateral condyle of the femur near the origin of the lateral head of the gastrocnemius and from the tendon of origin of that muscle. It forms a thin tendon which lies on the medial side of the tendo Achilles in the lower part of the leg. It is inserted into the plantar fascia. In some specimens the tendon fuses with the tendo Achilles, and in two specimens the muscle was so blended with the lateral head of the gastrocnemius that it was impossible to separate the two muscles.

M. Flexor Longus Digitorum Tibialis arises from the upper half of the posterior surface of the tibia and forms a tendon which passes below the medial annular ligament. In the middle of the sole over the middle of the shafts of the third and fourth metatarsals the tendon fuses with the fibularis tendon to the digits. From the medial side of the tendon a thin tendon arises which is the only long flexor of the hallux. The flexor hallucis longus is therefore absent as a separate muscle.

M. Flexor Longus Digitorum Fibularis arises from the postero-medial aspect of the fibula and from the interosseous membrane. It lies deep to the above flexor in the leg, behind the annular ligament and in the sole. It fuses with the tibialis over the metatarsals of the third and fourth digits. The tibialis tendon gives rise to two tendons, one to the little toe and the other to the second digit. The tendon of the fibularis gives rise to the long flexor tendons of the third and fourth toes.

Flexor Digitorum Brevis.—This muscle has been described by Schauflihausen in seven specimens of *Hapale*, and in each there is some variation. In two specimens which were dissected the flexor arises from two heads of origin—a superficial from the tuberosity of the os calcis; this belly of muscle forms almost entirely the short flexor to the second toe. The deep head arises from the flexor tendons, and forms three tendons which split to allow the long flexor tendons to perforate them. They are inserted into the base of the second phalanx of the digits. In two other specimens accessory heads for the short flexor to the second toe were seen; these arose from the medial side of the long flexor tendon, and were inserted in one case into the medial side of the base of the second phalanx of the second digit, and in the other case into the flexor tendon.

The lumbricals and the interossei call for no special comment. There is a transverse head for the adductor hallucis, but the other short muscles of the hallux, with the exception of a small abductor hallucis, are absent. The abductor digiti quinti is present as a well-marked muscle mass, and is inserted into the head of the first phalanx.

Ocular Muscles.

The extrinsic muscles of the eyeball have been described briefly by Otteley (1879) for most of the Primates. The conditions which I have found in *Hapale* do not differ much from his account.

The retractor bulbi, which Otteley remarks is absent in *Hapale*, is present in two of the eyes which were dissected. It is a very thin slip, but it was undoubtedly muscular, as sections showed. It was supplied by the sixth nerve.

The external rectus was inserted into the eyeball midway between the equator and the corneo-sclerotic junction. The internal rectus was inserted slightly closer to the corneal junction than the external rectus. The interesting differences between the insertions of the muscles of *Hapale* and those in the Lemurs was found in the direction of insertion of the superior oblique and its relation to the insertion of the superior rectus. The latter muscle was inserted well back on the upper surface of the eyeball almost on the equator. The line of insertion is not parallel to the corneo-sclerotic junction, but almost at right angles to it. Close behind this insertion and parallel to it is the insertion of the superior oblique. This latter muscle arises in the usual manner and passes through a pulley on the inner side of the superior orbital margin. The inferior rectus is inserted along the line of the equator or slightly in front of it. The inferior oblique is arising from the superior maxilla close to the lachrymal foramen, and is inserted into the eyeball close to the optic nerve. The general arrangements of the eye muscles are closely similar to those seen in *Tarsius*, and there is little doubt that the reason for the slight movements of the eye in the orbit is to be found in the great mobility of the head on the neck. In this way the two animals are closely similar.

Knee-Joint.

The structure of the knee-joint in *Hapale* has been studied by Forster (1904) and by van Westrienen (n. d.). The latter author has compared the conditions found in *Hapale* with most of the other Primates and with the human condition. She has investigated the subject so thoroughly that my work has been but a confirmation of the observations which she has made.

Three points deserve special attention. First, the nature of the origin of the gastrocnemii; second, the relation of the semi-membranosus tendon to the joint capsule; and, thirdly, the attachments of the menisci to the bones forming the joint.

The actual origin of the gastrocnemius lateralis is from a small mass of cartilage or bone and from a small area of the capsule. The sesamoid bone is actually embodied in the outer wall of the joint capsule. From this bone two bands of fibres arise—one, which is short and strong, is attached to the posterior aspect of the lateral condyle of the femur, and a medial band which pass downwards along the posterior surface of the joint capsule and is

attached to the tibia between the two condyles of that bone. This constitutes the lateral oblique ligament. The medial head of the gastrocnemius arises in a similar way to the lateral head. The fibres which are arising from the capsule in the case of the lateral head are now absent or very small in number. The origin of the head is thus migrating towards the femur. The band of fibres from the sesamoid running obliquely downwards are indistinct. These fibres lie deep to fibres derived from the semi-membranosus tendon. The condition in *Hapale* is thus intermediate between the lemurine one and that seen in the joint capsules of other Platyrrhines and also in Anthropoids. In the Lemurs both oblique ligaments are well developed and there is no incorporation of the semi-membranosus of the capsule. The fibres of the semi-membranosus in *Hapale* lie on the posterior surface of the joint capsule and are incorporated in this wall. The direction of the fibres is downwards superficial to the medial oblique ligament from the medial sesamoid. They then pass laterally and upwards to fuse with the lateral oblique ligament. In this way they obtain a distinct insertion into the lateral sesamoid. The small transverse fibres which bind the two oblique ligaments together near their tibial insertion are weak. This condition is intermediate between the condition in *Lemur macaco*, where the semi-membranosus has no connection whatsoever with the joint-capsule, and that found in the Spider Monkey.

The general shape of the menisci resembles the condition in Man. The lateral meniscus is C-shaped as in Man. Anteriorly it is attached by a strong band of fibres to the tibia between the anterior cruciate ligament and the intercondylar eminence, and posteriorly it is attached to the tibia a short distance in front of the attachment of the posterior edge of the medial meniscus. There is also a strong attachment to the femur through the lateral menisco-femoral ligament. The medial meniscus is more open or crescentic in shape than the lateral meniscus. It is attached anteriorly to the tibia immediately in front of the attachment of the anterior cruciate ligament. Posteriorly there is an attachment to the tibia posterior to the attachment of the posterior horn of the lateral meniscus and in front or anterior to the attachment of the posterior cruciate ligament. There is no connection with the femur.

The condition of the menisci is a distinct advance on the lemurine form, where each meniscus is attached through its posterior horn with the femur. In *Hapale* the condition that I found was identical with that described by Westrienen.

THE CIRCULATORY SYSTEM.

The Heart.

The pericardial sac is a thin sero-fibrous bag which completely invests the heart and is continued above over the roots of the great vessels. It is attached anteriorly to the deep surface of

the sternum, laterally it is covered by the pleural sacs, and inferiorly it is separated from the diaphragm, except near the apex, by the infracardiac recess of the right pleura. When the pericardium is removed the anterior surface of the heart is seen to consist of the right ventricle, the right auricle with its appendage, and a part of the wall of the left ventricle. The apex of the heart is formed by the left ventricle. The right surface of the heart is formed by the right auricle. The inferior surface consists almost entirely of the right ventricle and a very small portion of the apex of the left ventricle. The left surface is formed by the left ventricle and the lower part of the left auricle. The posterior surface is formed by the left auricle. The left auricular appendage passes anteriorly towards the anterior surface of the heart, where a small part of it is visible.

The boundaries between the auricles and the ventricles are clearly marked. The right and left auricle are separated from each other by a shallow groove. The auricular appendages are about the same size and are triangular in shape. They pass insensibly into the auricular wall.

Right Auricle.—The surface of the interior of the auricle is smooth except in the appendage, which is trabaculated with muscle tissue covered with endocardium. The superior vena cava enters the auricle at its uppermost limit, and the inferior vena cava at the lower border. The crista terminalis is well marked and there is a distinct tubercle of Lower. The sinus part of the heart consists of a tubular portion joining the terminations of the venæ cavæ. The fossa of the foramen ovalis is present with a limbus. The Eustachian valve of the inferior vena cava is present and the thebesian valve over the coronary sinus is well marked. The right auriculo-ventricular valve presents no feature, of interest.

Right Ventricle.—Anteriorly and inferiorly the ventricular wall is well trabaculated. Very few trabaculæ are seen on the septal wall. Connecting the septal wall with the anterior wall near the apex three or four fine tendinæ are found. There is no muscular moderator band. The pulmonary valve has the usual arrangement. The flaps are thin and membranous and there is no sign of corpora aurantii.

Left Auricle.—There are three openings into this auricle, one large and two small. The large opening is for the pulmonary vein from the right lung, and the two small openings are the openings of the veins from the upper and lower lobes of the left lung.

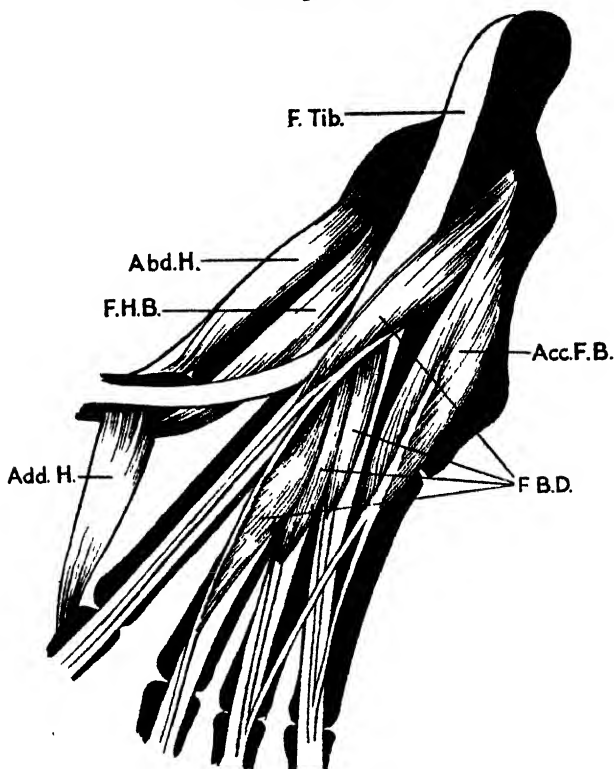
Left Ventricle.—The walls of this chamber of the heart are well trabaculated. There are no special features. The aortic-valve flaps are thickened near the upper or free edge, where there is a small nodule in the centre of each flap.

The heart lies in the thorax from the level of the articulation of the sixth costal cartilage with the sternum to the articulation of the cartilage of the third rib, and appears to be smaller

than the heart of *Tarsius* and of a squirrel-monkey of the same size.

The angle formed between the line joining the points of entrance of the venæ cavæ into the heart with the line joining the apex of the heart to the point of entrance of the superior

Text-figure 34.



The muscles of the sole of the foot.

Abd.H. Abductor hallucis M. Add.H. Adductor hallucis M. F.H.B. Flexor hallucis brevis. F.Tib. Flexor digitorum longus tibialis. Acc.F.B. Accessory flexor brevis muscle to the fourth and fifth toes. F.D.B. Flexor digitorum brevis. This specimen shows a well-marked short flexor for the hallux and a strong accessory flexor for the fourth and fifth toes.

vena cava is distinctly greater than that seen in *Tarsius*. In the latter animal it is about 45 to 50 degrees; in *Hapale* the angle approaches 60 degrees.

The coronary arteries are arranged in the usual primate manner. The coronary sinus is small and enters the right auricle. The entrance is protected by the thebesian valve.

The Pulmonary Circulation.

The pulmonary artery lies first on the left side, then behind the aorta, where it divides into the right and left pulmonary arteries. These arteries split up into lobar branches at the hilum of the lungs. Entering the lobes the artery of the lobe lies between the bronchus and the vein from the lobe. The arrangement of the lobar veins is peculiar. On the right side the lobar veins join together to form a single trunk which enters the posterior surface of the left auricle. On the left side the two lobar veins enter the left auricle close together, but as two distinct veins. This is intermediate between the *Tarsius* arrangement and that found in the higher anthropoids.

The Systemic Circulation.

The Great Vessels.—The ascending aorta is very short, about three to four millimetres in length. The vessel then passes backwards and to the left. From the upper surface of this transverse portion of its course the aorta gives off the three great vessels—the innominate artery, the left common carotid, and the left subclavian artery. After a short course the innominate gives off the right subclavian artery and continues on as the common carotid artery. The aorta, after giving off the great vessels, turns downwards along the left side of the spinal column and then gradually diverges to the right side. Along its course it gives off branches to the intercostal spaces, with the exception of the first space. It also gives off bronchial arteries which are very small. These enter the hilum of the lung and appear to be distributed mainly to the larger bronchi.

Abdominal Aorta and its Branches.

The celiac artery is a short trunk arising from the abdominal aorta shortly after it enters the abdomen. A small left coronary artery is given off near the origin of the trunk, and the trunk ends by splitting into two large arteries—the hepatic and the splenic. The hepatic artery supplies the arteries to the greater and lesser curvature of the stomach. These branches anastomose with the left coronary artery as in Man. The hepatic also supplies the pancreas and the descending loop of the duodenum. The artery then lies in the free edge of the lesser omentum, and on reaching the transverse fissure of the liver it breaks up into branches for each lobe of the liver. The splenic artery is large. It reaches the spleen through the lienorenal ligament. Short branches from the splenic pass to the great curvature of the stomach in the gastro-splenic omentum. These branches supply the greater curvature of the stomach in the region of the fundus and the body.

The superior mesenteric artery arises from the abdominal aorta immediately caudal to the celiac axis. It is a single trunk which passes into the root of the mesentery and breaks up into branches

to supply the ascending loop of the duodenum, the small intestine, and the colon as far as the splenic flexure. The right colic branch supplies the terminal ileum, the proximal part of the ascending colon, and the cæcum. The middle colic supplies the whole of the transverse colon and anastomoses with the left colic branch of the inferior mesenteric artery.

The inferior mesenteric artery arises from the abdominal aorta below the origin of the left renal artery. It forms a trunk which runs in the mesentery parallel to the long axis of the gut and gives off a large left colic artery and several smaller arteries to the colon and rectum. Near the termination of the gut a large hæmorrhoidal branch is given off, and the artery then breaks up into a number of small short branches.

The suprarenal artery arises as a single trunk from the lateral aspect of the abdominal aorta after the celiac artery has been given off. The artery is large for the size of the organ supplied by it.

The renal arteries arise from the aorta between the origin of the superior mesenteric and the inferior mesenteric arteries. There is a single vessel for each kidney. The vessel does not divide until it has passed into the hilum of the kidney.

The ovarian arteries arise from the anterior aspect of the aorta at the level of the lower pole of the kidney. They lie in close relation to the ureter, and pass into the pelvis in a fold of peritoneum which becomes the ovarico-pelvic ligament. They are distributed to the ovary, but appear to anastomose to some extent with the vessels of the Fallopian tube in the mesovarium.

The spermatic arteries and the spermatic veins follow the same course as the ovarian arteries as far as the brim of the pelvis. At this point the spermatic vessels diverge and enter the internal abdominal ring, through which they pass to be distributed to the testis and epididymis.

The abdominal aorta before dividing into the two common iliac arteries gives off the ilio-lumbar artery, which runs laterally and then along the lateral femoral cutaneous nerve into the thigh. The subcostal arteries and the lumbar segmental arteries are given off from the posterior surface of the vessel and are distributed in the normal way.

At the level of the junction of the fifth and sixth lumbar vertebrae the aorta divided into the two common iliac arteries. From the posterior surface of the vessel at the bifurcation the single middle sacral artery is given off. This vessel lies on the ventral surfaces of the caudal vertebrae and supplies the ventral muscles of the tail.

Vessels of the Inferior Extremity.

Manners-Smith has described the arteries of the leg in *Hapale pencillata*, and the condition found in *Hapale jacchus* appears to be identical with his findings.

The external iliac artery gives off the ilio-lumbar artery which has been described above, and at the same point the internal iliac artery arises and passes into the pelvis, where it breaks up into a lateral and medial division. The lateral branch supplies the structures of the lateral pelvic wall, and a small branch leaves the pelvis with the great sciatic nerve. The medial branch runs forwards and supplies the bladder. The artery in the female gives off the uterine artery which runs along the lateral wall of the uterus in the broad ligament. The remains of the obliterated hypogastric arteries are seen as two fine strands of tissue lying lateral to the urachus, and fade out near the tip of the urachus.

Near the germination of the external ilia a short trunk arises from which diverge three arteries. The inferior epigastric artery, which courses medially and has its usual relation to the inguinal canal, the obturator artery, which crosses the brim of the pelvis in the same relations as the abnormal obturator artery of human anatomy, and the third branch is the medial circumflex artery of the thigh. This artery passes into the thigh and then dips between the pectineus and the psoas, and supplies the muscles on the medial side of the hip-joint. In the upper part of the thigh the femoral artery gives off a large branch—the profunda femoris; from this arises the lateral circumflex artery. This breaks up almost immediately into an ascending and descending branch. These supply the vasti muscles on the lateral surface of the thigh. The profunda is a purely muscular artery, and descending along the medial side of the femur supplies the muscles on that aspect of the thigh.

The femoral artery divides into two in the lower part of Hunter's canal—the saphena artery and the popliteal artery. The saphenous artery runs along the inner side of the knee, and at the junction of the upper and middle thirds of the leg divided into an anterior and posterior branch. The posterior branch is the posterior tibial artery. The anterior branch splits into a superficial and a deep branch about the middle of the leg. As in Popowski's specimen, the branches formed an arch on the dorsum of the foot. The superficial arch gave off the common digital arteries, and the deep arch the dorsal metatarsal arteries to the second and third clefts. The latter arteries do not reach the digits.

The popliteal artery gains the posterior part of the leg by passing deep to the adductor magnus. In the popliteal region the distribution of the articular arteries is by no means constant. Popowski describes two different conditions—one in *H. jacchus*, where there is an a. genu lateralis and an a. genu medialis, each of which subdivides into superior and inferior branches. In his specimen of *H. pencillata* there is an a. genu superior dividing into a medial and lateral branch and an a. genu inferior dividing into an a. medialis and an a. genu media. Manners-Smith describes in his specimen an a. genu superior lateralis and an a. genu medialis. He also describes a sural artery. The condition found

in the injected specimen appears to be similar to that described by Popowski in his *H. jacchus*. The artery terminates by dividing into the anterior tibial and the peroneal arteries.

The posterior tibial artery passes along the back of the calf deep to the gastrocnemius and the soleus, and passes into the sole of the foot, where it becomes the medial plantar artery. In the sole it divides to supply the short flexors, and ends by supplying the clefts between the hallus and the first digit and that between the second and the third digits.

The peroneal artery supplies the peronei muscles and does not extend as a recognisable vessel beyond the middle of the leg.

The Arteries of the Upper Extremity.

The subclavian artery becomes the axillary artery after the vessel has crossed the first rib. In the axilla the arrangement of the vessels is very variable, and many different descriptions have been given of these. Manners-Smith has summarised the previous findings in his paper. The condition described below is based on one single specimen dissected. The superficial brachial artery arises from the axillary soon after it enters the axilla. It gives off two branches—a thoraco-acromial and a lateral thoracic artery. These are distributed in the manner described in human anatomy. The deep brachial (*a. brachialis profunda*) artery is the remainder of the axillary artery, and from it arise either separately or from a common trunk the circumflex humeral arteries and the subscapular artery. Lower down the arm the artery gives rise to the *a. profunda brachii* (the superior profunda) artery. The profunda brachii divides into the *a. collateralis radialis* (the anterior branch of the superior profunda); on one side this artery came off from the posterior humeral artery and the *a. collateralis media*.

The brachialis superficialis lies in the sulcus between the biceps and the triceps on the medial side of the arm; in this part of its course it lies superficial to the median and ulnar nerves. Above the elbow the transverse cubital artery arises which lies between the brachialis and the humerus. The artery is continued on into the forearm superficial to the biceps tendon as the radial artery. It divides into a superficial and a deep branch. The superficial branch or palmar branch passes into the palm, where it becomes the superficial volar artery. The dorsal or deep branch passes deep to the abductor pollicis longus and reaches the dorsum of the wrist.

The *a. brachialis profunda* lies in relation to the median nerve as far as the elbow. At this point the artery divides into two, the ulnar and the interosseus artery. The ulnar artery has its usual relations in the forearm. On reaching the palm it forms, with the palmar branch of the radial, the superficial palmar arch from which arise the arteries to the digital clefts. These in turn subdivide to form the common digital arteries. The small branch

to the ulnar side of the hand supplies the muscles of the hypothenar eminence.

The interosseus artery divides into a volar and palmar branches which lie along the interosseus membrane and supply the muscles of the forearm.

The Vessels of the Neck.—The common carotid artery continues into the neck as high as the great cornu of the hyoid bone before it subdivides into the external and internal carotid arteries. The external carotid immediately subdivides into the lingual, superior thyroid, facial, internal maxillary, and superficial temporal artery. The internal maxillary artery is small, but the superficial temporal artery is large.

The course of the internal carotid is described in the section on the ear. The muscles of the neck are supplied by the branches of the vertebral artery.

Venous System.

The venous system calls for no special comment. The arrangement of these vessels corresponds to the general primate pattern.

Lymphatic System.

Silvester has shown that the lymphatic system of the Marmoset is arranged in the same manner as that in the South American Monkeys. These animals differ from the Old World Monkeys and Anthropoid Apes in that there are connections with the venous system in the region of the junction of the renal veins with the inferior vena cava. The lymphatics which enter the veins in this region are the terminal vessels which drain the whole of the abdominal viscera, the pelvic organs, and the whole of the lower half of the body below the level of the umbilicus. I have not been able to obtain sufficiently definite results by injection methods to confirm the statements of Silvester. The lymphatics of the upper half of the body are arranged in a manner common to that in all the other primates.

THE DIGESTIVE SYSTEM.

Teeth.—The teeth are described under the skull.

Tongue.—Sonntag in his monograph has described the papillæ of the tongue and their distribution (P. Z. S. 1922, pp. 517-524). The tongue is a thin muscular organ tapering gradually from base to the tip, which is truncated and rounded. The tip is covered with fungiform papillæ. On the ventral surface there is a well-marked groove in the middle line. This groove opens out to form a triangular space to the base of which the anterior edge of the frenum is attached. The frenum is formed of two triangular folds of mucous membrane which are joined anteriorly to form a free edge. Laterally and posteriorly they diverge and are attached along the floor of the mouth and to the ventral surface of the tongue. At the inferior part of the lateral surface of the frenum

two folds spring out which have a serrated or scalloped edge. These folds join in front of the anterior edge of the frenum in a bifid tip.

On section the tongue shows in its posterior half a well-marked fibrous median septum or raphe. This raphe gradually disappears as it is traced forward. Posteriorly it is attached to the hyoid bone in the middle line. The muscle-tissue of the tongue consists of intrinsic fibres and extrinsic fibres. The extrinsic muscles have been described in the section on the anterior region of the neck. The fibres of the genio-glossus pass into the tongue on its ventral surface in the posterior third. They form fibres running upwards and forwards in the tongue towards the tip. They pass between all the other muscles to reach the dorsum. The fibres of the stylo-glossus enter the lateral aspect of the tongue and run horizontally forwards towards the tip. The fibres of the hyoglossus lie along the inferior and lateral region of the tongue and appear to form longitudinal bundles lying near the ventral surface. They eventually reach as far as the tip. The intrinsic muscle fibres are arranged in four groups: (*a*) the dorsal longitudinal fibres, (*b*) the ventral longitudinal fibres, (*c*) the transverse fibres, and (*d*) the ventral or oblique fibres. The dorsal longitudinal fibres lie close beneath the submucous tissue of the dorsum. The ventral longitudinal fibres lie along the ventral surface and in the sublingua. The transverse fibres run from the lateral margins of the tongue inwards and downwards towards the ventral surface. Some of these fibres appear to arise from the side wall of the pharynx and the soft palate and enter the tongue in its posterior third. The vertical fibres are irregularly arranged throughout the whole of the tongue. They are the weakest of all the intrinsic muscles.

Lingual glands are present, but no apical glands of Nuhn can be detected.

Palate.—The hard palate is traversed by six transverse ridges composed of folds of mucous membrane. These are found on the anterior region, and only two of them form a complete ridge across the middle line. The posterior four become smaller and diverge from the middle line as the posterior margin of the palate is approached. All the ridges are covered with papillæ. The soft palate is very extensive. It extends posteriorly and forms the boundary between the mouth and the pharynx. The bucco-pharyngeal opening is small. On the summit of the arch a small tubercle is seen, this is the uvula. It is bifid and appears to be composed entirely of mucous and submucous tissue alone.

Pharynx.—The naso-pharynx is narrow antero-posteriorly. The whole of the anterior boundary is taken up by the posterior nares. On the lateral walls near their posterior margins the Eustachian tubes are open. The openings of the Eustachian tubes are surrounded by an elevation caused by the medial ends of the tubal cartilages. There is no sign of a definite pharyngeal tonsil, but in the submucous tissue of the roof and the posterior-wall

there is a collection of lymphoid tissue. In some specimens this is absent.

The oral pharynx calls for no special comment. The palatine tonsil is described below. The anterior pillar of the fauces is composed of mucous membrane covering a mass of muscle which is derived from the soft palate and which runs into the lateral surface of the tongue. The posterior pillar is formed by a small bundle of muscle fibres running from the soft palate into the lateral wall of the pharynx.

On the anterior wall of the laryngeal pharynx the epiglottis is attached. This cartilage projects upwards and is plainly visible when the mouth is opened. Laterally between the ary-epiglottidean folds and the medial surface of the thyroid cartilage is a space which is homologous with the pyriform recess of the human anatomy.

Muscles of the Pharynx.—Three sheets of muscle surround the pharyngeal cavity, and into this mass of muscle fibres are inserted from other sources. These extrinsic muscles are derived from the stylo-pharyngeous and the palato-pharyngeous. The proper muscles of the pharynx are the three constrictor muscles.

The superior constrictor obtains fibres from the side of the tongue, in its posterior third, a few fibres from the mandible behind the third molar tooth, from a raphe extending from this point to the lowest point of the pterygoid plate and from the pterygoid plate itself. The fibres sweep posteriorly. The upper fibres incline upwards and are inserted into the median raphe of the pharynx, which extends from the base of the skull to the upper part of the œsophagus. The lower fibres extend backwards, and the lowest fibres pass downwards as well as backwards and are inserted into the raphe.

The middle constrictor arises from the hyoid bone, and expanding fanwise it is inserted into the median raphe. The upper fibres lie superficial to the lowest fibres of the superior constrictor. The superior laryngeal artery and nerve pass below the lower border of the middle constrictor to reach the interior of the larynx.

The inferior constrictor arises from the curved crest on the lateral surface of the thyroid cartilage and is inserted into the median raphe. The upper fibres are inserted into the raphe superficial to the fibres of the lower constrictor. The lower fibres of the inferior constrictor are continuous over the lateral wall of the œsophagus and blend with its outer longitudinal muscle coat. The recurrent laryngeal nerve passes under the lower border of the inferior constrictor.

Tonsil.—The tonsil of *Hapale* has been described by Hett. It is a very simple pocket with lymphoid tissue developed around the diverticulum. The arrangement of the tissue is seen in a section through the organ. There is a well-marked supra-tonsillar recess. The tonsil appears to be of a fairly constant size in all the animals which were examined. Animals with a complete

dentition (permanent) which shows signs of wear have a tonsil equally well developed as those who are just erupting their third molar tooth.

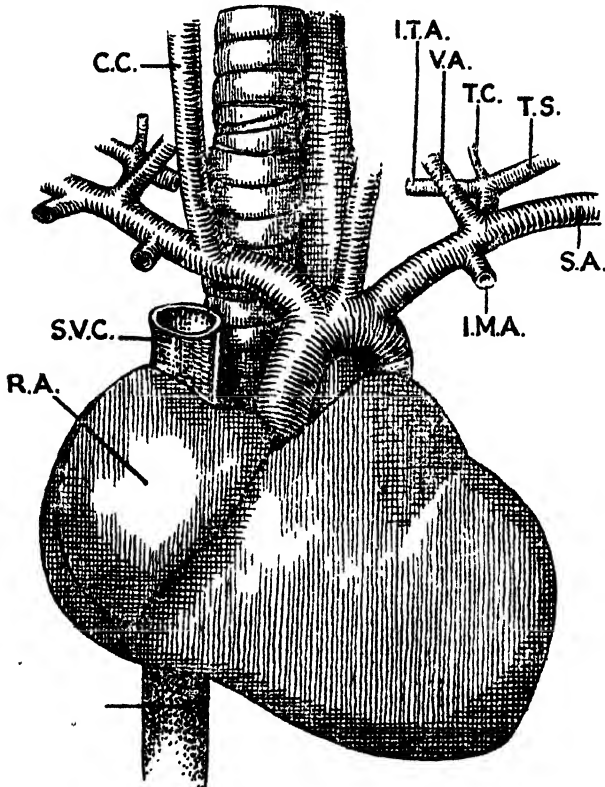
Salivary Glands.—The submaxillary gland is the largest of the three glands present in *Hapale*. It lies along the lower edge of the mandible in the region of the angle. It extends upwards in contact with the deep surface of the internal pterygoid muscle, and downwards into the anterior part of the neck. It is often divided into two lobes—an anterior and a posterior. The parotid gland is smaller than the submaxillary. It lies in front of and below the external auditory meatus and extends forwards over the posterior edge of the masseter muscle on to the face. From its anterior edge the duct arises. This pierces the buccinator muscle and the mucous membrane of the mouth about the level of the last pre-molar tooth of the upper jaw. The sublingual gland is not enclosed in a capsule as are the other glands. It consists of a mass of gland acini which lie under the mucous membrane of the floor of the mouth, lateral to the frenum. The acini pass between the muscles forming the floor of the mouth, and some lie along the deep surface of the mandible.

Œsophagus.—In the neck the Œsophagus lies in the middle line deep to the trachea. On reaching the thorax it bends to the right side until it reaches the level of the bifurcation of the trachea. There it deviates to the left side and pierces the diaphragm in its left posterior muscular part. In the abdomen the Œsophagus lies first in a deep sulcus in the posterior surface of the liver. Issuing thence it is almost immediately continuous with the stomach. The cardio-Œsophageal junction is oblique and is situated at the upper limit of the lesser curvature. On the left of the termination of the Œsophagus the fundus of the stomach rises up lateral to it. The microscopic structure is identical with that of Man. The longitudinal coat of muscle shows many striated fibres in the upper half of the Œsophagus. The epithelium is arranged in the typical squamous manner. The squamous epithelium ends abruptly at the cardio-Œsophageal junction.

Stomach.—The stomach varies in form in each of the specimens, but the main features are constant. The organ can be divided into four parts—the fundus, the body, the pyloric canal, and the pyloric antrum. The fundus extends upwards lateral to the Œsophagus. It is relatively large. The body is continuous above with the fundus, from which it is not separated by any anatomical feature on the greater curvature of the stomach. In shape the body varies with the amount of food in the stomach at the time of death and also on whether the animal is examined fresh or after injection. In injected specimens, injected soon after death, the body is tubular and is separated from the pyloric antrum by a groove. This groove forms the incisura angularis on the lesser curvature of the stomach. The incisura can be distinguished in nearly every specimen. The body is continuous with the pyloric

antrum, which is usually a tube of smaller diameter than the body. This part merges into a narrow short tube—the pyloric canal—from which is separated, only by a faint constriction, the sulcus intermedius. The pyloric canal ends at the pyloric

Text-figure 35.



The anterior view of the heart and great vessels.

C.C. Common carotid artery. I.T.A. Inferior thyroid artery. V.A. Vertebral artery. T.C. Transverse cervical artery. T.S. Transverse scapular artery. S.A. Subclavian artery. I.M.A. Internal mammary artery. S.V.C. Superior vena cava. R.A. Right auricle.

sphincter. The pyloric sphincter is frequently relaxed after death, but when contracted it forms a groove on the outer surface of the gut. The stomach is situated in the abdomen under cover of the liver. Only a small part of the anterior surface is in contact with the anterior abdominal wall.

Small Intestine.

Duodenum.—The duodenum forms a J-shaped loop. The long limb descends in contact with the visceral surface of the right lower lobe of the liver and the upper pole of the right kidney. The transverse part is short and runs to the left, where it bends upwards to form the ascending part. The two latter parts hook round the lower border of the root of the mesentery. The usual first part of the duodenum is very short. The duodenum ends at a sharp flexure lying below the transverso meso-colon to which it is attached by a peritoneal band. The common bile-duct and the pancreatic ducts enter the descending limb of the duodenal loop at the junction of the upper third with the lower two-thirds. The loop has a definite meso-duodenum. In this mesentery the head and body of the pancreas are found. The anterior surface of the descending part of the duodenum is adherent to the upper layer of the transverse meso-colon. The transverse colon is itself adherent to the duodenum where it crosses the descending loop. From the upper part of the meso-duodenum a short peritoneal band passes backwards to the inferior vena cava. This band forms the lower limit of the large foramen of Winslow.

Jejunum and Ileum.—There is no division of the remaining portion of the small intestine into two parts—jejunum and ileum. The intestine forms three short loops which have their concavities directed downwards and to the right. The terminal ileum passes downwards parallel to the medial edge of the ascending colon and then forms a small loop. The ileum joins the colon from below and on its medial side. The junction is oblique, and the circular muscle of the small intestine becomes thickened at the junction to form a sphincter.

Large Intestine.—The large intestine is long and equals in length the crown-rump height of the animal. It forms an inverted U-shaped loop. The right limb consists of the cæcum and the ascending colon. The cæcum is about four centimetres long. Commencing at the ileo-colic junction the cæcum enlarges slightly towards its termination, which is hooked on itself round the end of the narrow meso-cæcum. There is no sign of any appendix vermiformis. The termination of the cæcum lies in the lowest part of the abdominal cavity. The ascending colon is slightly shorter than the cæcum. At the abdominal surface of the liver it turns to the left and becomes the transverse colon. The transverse colon forms an arch with its convexity forwards towards the anterior abdominal wall. On the left side this part of the large intestine becomes bent on itself acutely to become the descending colon. This flexure of the colon is not attached to the abdominal wall by peritoneal ligaments. The descending colon passes downwards along the left side of the abdominal cavity. It passes insensibly into the rectum and is continued on to the anus. This part of the gut is a straight tube without any sign of flexures.

The Peritoneum.

Ventral Mesentery.—The ventral mesentery is split by the liver into two parts—the hepatic ligaments and the lesser omentum. The peritoneal ligaments of the liver are thin folds lying close together without enclosing any considerable space between their layers. Hence there is no bare area of the liver. The falciform ligament is a thin fold of peritoneum attached ventrally to the upper half of the inner surface of linea alba. The upper attachment is continued backwards on to the diaphragm as far as the inferior vena cava. From this attachment the ligament passes to the upper surface of the central lobe of the liver, to which it is attached. The lower edge of the ligament, from the anterior abdominal wall to the liver, is free. The lesser omentum has a free edge on its right side from the transverse fissure of the liver to the highest point of the duodenum. To the left it is attached above to the transverse fissure of the liver, and below to the lesser curvature of the stomach. The free edge forms the free edge or the anterior boundary of the foramen of Winslow, and in it run the common bile duct, the hepatic artery, and the portal vein. The lower boundary is formed by a fold from the meso-duodenum to the inferior vena cava.

Dorsal Mesentery.—The dorsal mesentery leaves the dorsal wall of the abdomen where the œsophagus joins the stomach. It forms a large fold of peritoneum attached above to the greater curvature of the stomach and to the upper part of the duodenum. This fold in its right portion is the great omentum, to the left the fold splits to include the spleen. From the spleen the two layers of the fold unite to form the lienorenal ligament, which passes medially to the posterior abdominal wall medial to the supra-renal body and the kidney of the left side. From this point the two layers are attached transversely along the abdominal wall above the base of the transverse mesocolon as far as the mesoduodenum. This continuous sheet of peritoneum thus encloses a space which is part of the lesser sac of the peritoneum. The transverse mesocolon is not fused to the posterior layer of the great omentum.

The Mesentery of the Intestine.—The mesoduodenum is described above, along with the description of the duodenum. The mesentery of the small intestine arises around the superior mesenteric artery from a small area between the vertical part of the pancreas and the ascending limb of the duodenal loop. It is continuous with the mesentery of the ascending and transverse colon, which arise from the same area. The mesentery of the descending colon and the rectum arises from the mid-dorsal line as far as the lower rectum. These mesenteries are continuous with the mesentery of the small intestine and the proximal part of the large intestine. It will be seen that there is in *Hapale* a continuous common mesentery for the whole of the intestine with the exception of the duodenum, which has a separate mesoduodenum. The cæcum has a small fold of peritoneum passing along its medial border. This fold is derived from the mesentery

of the terminal ileum and contains the vessels and nerves to the cæcum.

Pancreas.—This organ consists of a vertical and transverse portions. The vertical portion lies in the meso-duodenum and is continuous above with the transverse portion which stretches across the middle line in the base of the attachment of the great omentum to the posterior abdominal wall. To the left the transverse portion comes into contact with the medial margin of the left suprarenal gland and the left kidney. The vertical part corresponds to the head, and the transverse part to the tail, of the human pancreas.

Liver.—The liver is relatively small compared to the liver in *Tarsius*. *In situ* only a small part of the central lobe is seen appearing under the sub-costal arch. In its arrangement it is exceedingly simple. The lobes and the fissures closely approximate to the condition found in *Nycticebus*. It is divided into four lobes :—

- (a) Central.
- (b) Left.
- (c) Right.
- (d) Caudate.

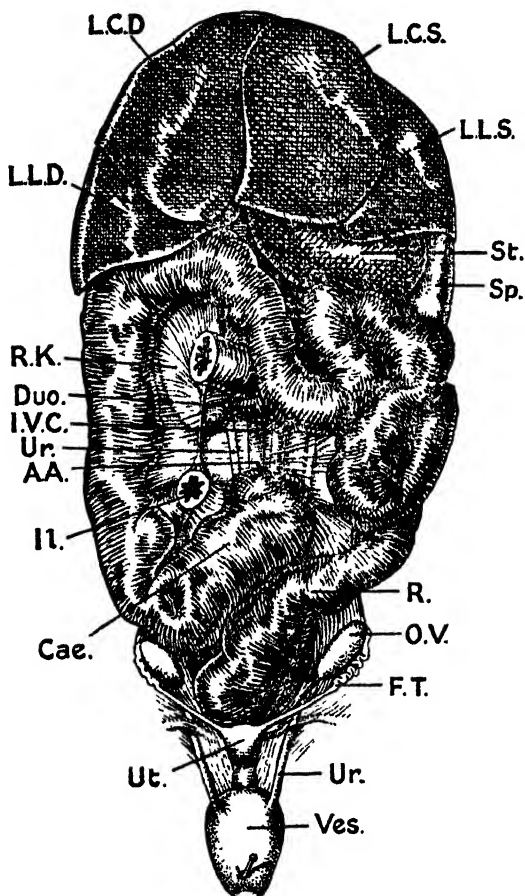
These correspond respectively to the central, left lateral, right lateral, and the caudate lobes described by Ruge in *Nycticebus*.

The central lobe occupies most of the subphrenic surface. It is divided into right and left halves by a fissure—the incisura umbilicalis of Ruge. The falciform ligament continues this division backwards. The fissure extends on to the visceral surface of the lobe. On the surface of the right half of the central lobe there is a deep fossa to lodge the gall-bladder. The gall-bladder is not buried in liver tissue. The remainder of the visceral surface is in contact with the upper or ventral surface of the stomach. On the upper surface of the lobe the inferior vena cava issues out of the liver. The ligaments of the liver radiate from this point in three directions—ventrally the falciform ligament, laterally to the left the left coronary ligament, and laterally to the right the right coronary ligament. The central lobe is separated from the left lobe by a deep fissure on the upper visceral and posterior surfaces, leaving only a small attachment to the left lobe. The central lobe overlays the upper surface of the left lobe, which lies inferior and lateral to the central lobe. The lateral surface of the left lobe is in contact with the diaphragm and the lateral abdominal wall. The visceral surface is in relation to the following organs:—the fundus of the stomach, the spleen, the left supra-renal gland, and the splenic flexure of the colon.

The œsophagus lies in a fissure between the left lobe and the caudate lobe of the liver. The left coronary ligament extends downwards on the posterior surface to the lower edge of the lobe

(text-figure 37). The right lobe is the largest lobe. It is overlapped above by the central lobe. Its lateral surface is in contact

Text-figure 36.

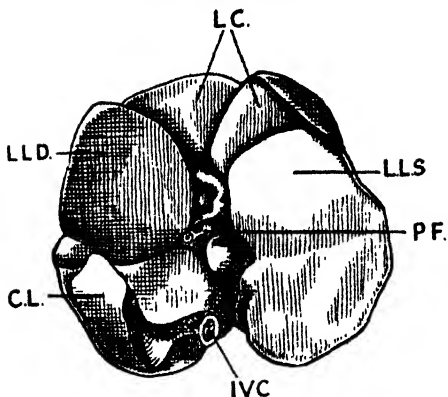


The abdominal viscera after removal of the small intestine. The bladder is drawn forward to expose the ureters.

L.C.D. Right central lobe of liver. L.C.S. Left central lobe. L.L.D. Right lateral lobe. L.L.S. Left lateral lobe. St. Stomach. Sp. Spleen. R.K. Right kidney. Duo. Duodenum. I.V.C. Inferior vena cava. Ur. Ureter. A.A. Abdominal aorta. Il. Ileum. Cæ. Cæcum. Ut. Uterus. Ves. Bladder. F.T. Fallopian tube. Ov. Ovary. R. Rectum.

with the right lateral surface of the diaphragm. Posteriorly the right coronary ligament passes downwards to the entrance of the inferior vena cava into the lower edge of the caudate lobe. The

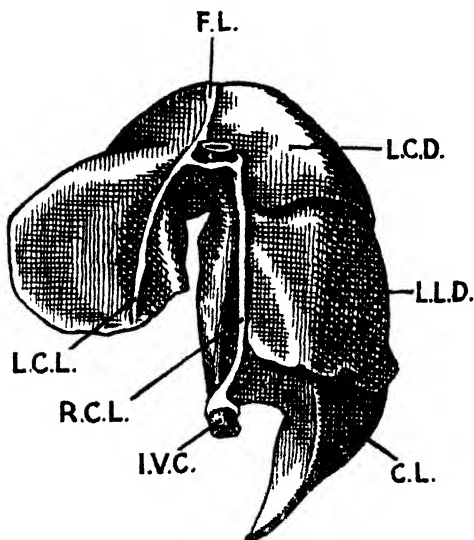
Text-figure 37.



The inferior view of the liver.

L.C. Lobus centralis divided into two parts by the umbilical fissure. L.L.D. Lobus lateralis dexter. L.L.S. Lobus lateralis sinister. P.F. Portal fissure. I.V.C. Inferior vena cava. C.L. Caudate lobe.

Text-figure 38.



The posterior surface of the liver.

F.L. Falciform ligament. L.C.D. Lobus centralis dexter. L.L.D. Lobus lateralis dexter. C.L. Caudate lobe. I.V.C. Inferior vena cava. R.C.L. Right coronary ligament. L.C.L. Left coronary ligament.

caudate lobe is divided off from the right lobe by a deep fissure on the visceral, lateral, and posterior surfaces. The fissure ends at the lateral edge of the right coronary ligament near its termination. At this point a groove continues the fissure upwards. To the bottom of this groove the right coronary ligament is attached. The caudate lobe shows on its inferior surface a deep fossa for the right supra-renal gland and a small part of the upper pole of the right kidney. In contact with the visceral surfaces of the right and caudate lobes there lie the pars descendens of the duodenum, the junction of the ascending and transverse colon. Laterally the caudate lobe reached the lateral abdominal wall. The small accessory lobes are absent.

The Diaphragm.—This muscle arises from :—

- (a) the upper three lumbar vertebræ, through the crura ;
- (b) the arcuate ligaments—medial and lateral ;
- (c) the ribs ;
- (d) the xiphoid process of the sternum.

The crura arise from the bodies of the first, second, and third lumbar vertebræ. They unite in the middle line and form the upper boundary of the aortic opening into the abdomen ; there appears to be no middle arcuate ligament. The fibres of the crura arch forwards and upwards into the central tendon. The medial arcuate ligaments arch over the psoas muscles. The lateral arcuate ligaments connect the first lumbar vertebra to the last ribs and arch over the quadratus lumborum. From these fibres pass upwards parallel to the crural fibres and are inserted into the postero-lateral parts of the central tendon. From the costal cartilage of the fifth to the ninth ribs and from the tips of the tenth, eleventh, and twelfth ribs, slips arise which pass almost vertically upwards and then arch inwards to be inserted into the central tendon ; the short slip which arises from the xiphoid process is inserted into the anterior part of the central tendon.

The central tendon of the diaphragm is trefoil in shape. The right and left parts are relatively narrow, but the ventral leaf is broad. Through this ventral portion the inferior cava passes from the abdomen to the thorax. The outer wall of the vessel is bound to the tendon by dense fibrous tissue. The tendon is separated from the pericardial sac except over the apex of the sac, which is in contact and fused with the diaphragm. The greater part of the pericardium is separated from the diaphragm by the infra-cardiac recess of the right pleura for the azygos lobe of that lung. The œsophagus pierces the diaphragm posteriorly and is surrounded by muscle tissue which is derived from the crura. The tube is not bound to the diaphragm, as is the case with the vena cava. With the œsophagus pass the abdominal branches of the right and left vagus nerves. The aorta passes between the crura near their origins and is accompanied by the two azygos veins. The sympathetic trunk and the great splanchnic nerve enter the abdomen under the medial arcuate ligament.

THE RESPIRATORY SYSTEM.

The Larynx.

The cavity of the larynx is bounded above by the large epiglottis, the ary-epiglottidean folds, and the arytenoid cartilages. This upper boundary encloses a large space which narrows rapidly to the level of the false vocal folds. The anterior end of each vocal fold is often seen to be swollen out, and a similar swelling is seen near the posterior end. In this latter swelling the cartilage of Wrisberg is situated. On separating the false folds the true vocal folds are seen as thin membranous structures on the lateral wall of the larynx. Lying between the false and the true folds there is a distinct ventricle which passes outwards and backwards below the false vocal fold as far as the posterior edge of the thyroid cartilage.

The Cartilages of the Larynx.

Although the hyoid bone is not, strictly speaking, part of the larynx, it is important to describe it in detail at this point. It consists of a body and two pairs of cornua. The body is a thin bony plate which extends downwards in front of the thyroid cartilage to cover the upper two-thirds of this structure. The under surface of the bone is connected to the thyroid cartilage by a thin thyro-hyoid ligament. The body is continued backwards into the greater cornua, which are thin bars of bone extending backwards on either side of the laryngeal pharynx. They articulate with the superior cornu of the thyroid cartilage by a distinct joint. The lesser cornua are small and are often cartilaginous and not ossified. They are connected by a thin ligamentous band to the temporal bone in the region of the bulla. No cartilages are developed in this structure nor is there any sign of a styloid process, although this has been described by other observers.

Thyroid Cartilage.—This cartilage is made up of two quadrilateral plates of cartilage which are united in front in the middle line and make an angle of 60 degrees with each other. The cartilage in the middle line is thickened and gradually thins out as the posterior border is approached. The upper edge is prolonged into a blunt superior cornu which articulates with the hyoid. The inferior cornu is a downward prolongation of the posterior edge which articulates with the cricoid cartilage. The inferior edge of the thyroid cartilage is attached to the upper edge of the cricoid by the crico-thyroid ligament. This ligament is completely covered by the crico-thyroid muscle. The oblique line is replaced by a ridge of cartilage which commences below and in front along the lower border of the cartilage and is continued up in a crescentic manner to end well in front of the superior cornu.

Cricoid Cartilage.—The cricoid cartilage has the usual signet-ring shape. In the middle line it projects slightly in front of the

thyroid cartilage, and posteriorly it is expanded to form a well-marked lamina.

Arytenoid Cartilages.—These are small pyramidal structures which are perched on the upper edge of the posterior surface of the cricoid. It is stated by Lampert (1926) that the axis of the joint is horizontal. I have found that it is not quite horizontal, but that the axis is inclined slightly upwards and medially. The arytenoid cartilages are attached to the cricoid by strong ligaments. Near the apex of the cartilage there is a small processus vocalis. The apex is attached to the posterior end of the ary-epiglottidean and the false vocal folds.

Ligaments of the Larynx.—The epiglottis is connected to the base of the tongue by strong glosso-epiglottic folds which enclose small feebly-developed muscle strands. These muscle fibres are intermingled with the fibres which run from the base of the epiglottis to the body of the hyoid bone. The hyo-epiglottic fold is mainly a mucous fold and encloses the small amount of muscle fibres noted above.

The hyoid bone and the thyroid are attached by the thyro-hyoid ligament which is attached to the posterior surface of the body and to the upper edge of the thyroid cartilage. In places it is very weak.

The crico-thyroid ligament is strongly developed in the middle line in front and in the region of the inferior cornu of the thyroid cartilage. In the latter region it forms part of the capsule of the crico-thyroid joint. The crico-arytenoid ligaments are attached to the base of the arytenoid and from there to the antero-medial surface of the posterior part of the cricoid cartilage. They are only capsular ligaments for the joint between the two cartilages.

The false vocal fold is attached anteriorly to the internal aspect of the thyroid laminae. From there it sweeps backwards and slightly downwards to reach the cartilage of Wrisberg, which is well developed. Through this cartilage the fold is attached to the upper limit of the arytenoid cartilage by a strong ligament. The true vocal fold arises from the thyroid angle immediately inferior to the origin of the false fold. It runs backwards to be attached to the processus vocalis of the arytenoid cartilage.

Muscles of the Larynx.

The *Sterno-thyroid* muscle arises from the deep surface of the sternum below the origin of the sterno-hyoid. The fibres are inserted into the crest on the lateral surface of the thyroid cartilage.

The *Thyro-hyoid* muscle is very small owing to the close approximation of the hyoid to the thyroid cartilage. It is attached to the inferior border of the hyoid bone at the base of the great cornu and below to the thyroid cartilage at the base of the superior cornu. It is extremely thin.

Crico-thyroid muscle is a fan-shaped muscle which arises from the whole of the inferior edge of the thyroid cartilage and the anterior edge of the inferior cornu of the cartilage. The fibres are inserted into the cricoid cartilage and the two muscle masses meet in the middle line. The extent of the thyroid attachment varies slightly. The muscle fibres may be attached as far up on the lateral surface of the thyroid as the curved crest, and thus come to lie immediately inferior to the fibres of the sterno-thyroid muscle.

Crico-arytenoideus muscle.—The fibres of this muscle are arranged in two layers. The deeper layer is thin and consists of a few fibres which cross the middle line from one arytenoid cartilage to the one of the opposite side. These fibres are reported to be absent by Lampert, but they were seen in one fresh specimen dissected by me. The superficial part consists of oblique fibres which arise from the posterior surface and the medial border of the arytenoid cartilage and are inserted into the upper part of the cricoid cartilage in its posterior lamina. The fibres may in some part cross the middle line, but this is infrequent.

Thyro-arytenoid muscle is attached anteriorly to the angle of the thyroid cartilage near the inferior border and for a few millimetres above this. The muscle forms a single mass and is not divisible into an external and an internal portion. Hence there is no true vocalis. The muscle lies at the base of the true vocal fold and does not find its way into the fold, which is entirely membranous.

The muscles are supplied in the same way as the corresponding muscles in Man.

Trachea.

The length of the trachea varies slightly in the specimens examined. In the female it is about three centimetres and in the male about four or slightly less. There are thirty rings. Some of these are double, but no more than two double rings have been seen in any specimen. In specimens which have been fixed in formol the rings overlap posteriorly, but in the fresh animal there is a distinct gap between the dorsal ends of the rings. There is probably some smooth muscle connecting the ends of the rings. This has not been confirmed by sections.

The trachea divides into a right and a left bronchus. From the right main bronchus a branch arises which passes upwards into the upper lobe of the lung. This is the eparterial bronchus. Four main branches are given off to the right lung, that is one to each lobe. On the left side the bronchus splits into two, an upper and a lower branch.

Lungs.

The right lung consists of four lobes—an upper, ventral, lower, and azygos lobes. The upper lobe is folded over on

itself to produce a superficial and a deep lobule. In the same way the ventral lobe is folded over. The ventral lobe lies in relation to the right auricle. The lower lobe is the largest lobe. It lies in contact with the whole of the right cupola of the diaphragm and with the lateral thoracic wall as far as the fourth rib. The azygos lobe is L-shaped. The descending part lies in front of the lower part of the intra-thoracic portion of the œsophagus. The transverse limb crosses anterior to the œsophagus and posterior to the inferior vena cava. The transverse limb lies in the infra-cardiac recess of the right pleura which separates the right side of the heart from the diaphragm. The left lung consists of two lobes—an upper and a lower. These lobes are not subdivided by fissures.

Each lobe described above is supplied by a separate branch of the pulmonary artery, drained by a single vein and has a single branch of the bronchus running into it.

Pleural Cavity.

The right pleural cavity extends from a few millimetres above the level of the first rib downwards as far as the first lumbar vertebra on the scapular line. In front it extends to the level of the attachment of the sixth costal cartilage to the sternum. The infra-cardiac recess opens out from the lowest part of the medial wall of the sac. The left sac does not extend so far downwards as the right. It is invaginated on its medial wall by the apex of the heart.

THE UROGENITAL SYSTEM.

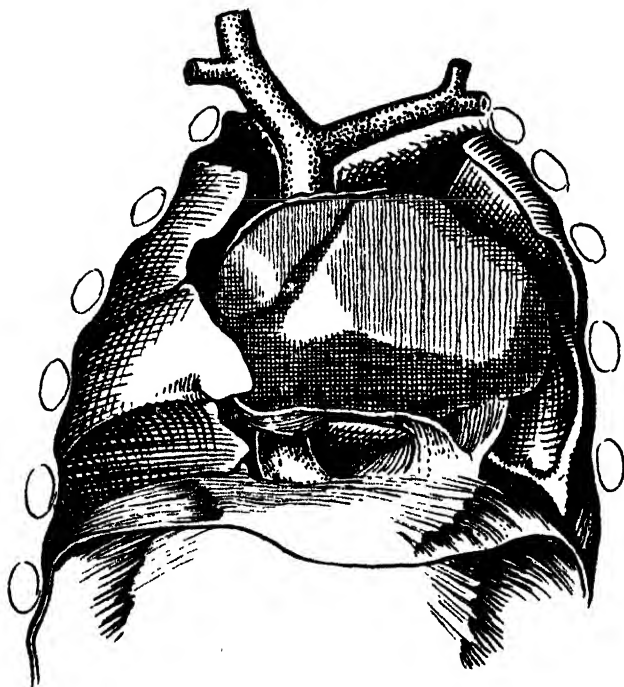
The Urinary Organs.

Kidney.—Both kidneys lie at the same level in the abdomen, from the second to the third lumbar vertebrae. They show no sign of lobulation. The upper pole is flattened for the suprarenal gland while the lower is more pointed. The general shape of the organ is “kidney-shaped.” The organ does not show any impressions on its surface for contact with neighbouring organs. The upper pole of the right kidney is in contact with the caudate lobe of the liver and the right suprarenal gland. The upper pole of the left is in relation to the suprarenal gland of that side and with the diaphragm. The lateral surface of the right kidney is in contact with the ascending colon, and the lateral surface of the left with the descending colon.

The hilum of the kidney lies on the medial surface midway between the upper and lower poles. There is no pelvis to be seen externally. The vessels and ureter emerge in a bunch from the hilum. On section, the pelvis is seen to be small and into its lateral wall a single large pyramid is invaginated. The apex lies almost at the hilum but does not project into the ureter. From the base of the pyramid the collecting tubules radiate to all parts of the kidney. The cortex is relatively thick.

The ureter is a single tube. It lies along the line of the apices of the transverse processes of the lumbar vertebrae to the brim of the pelvis, where it crosses the common iliac artery where the internal artery is given off. In the female the tube passes into the base of the broad ligament lateral to the vagina and so into the base of the bladder. In the male the vas deferens hooks round it before it enters the bladder.

Text-figure 39.



The thoracic viscera after the removal of the anterior part of the anterior wall of the pericardial sac. The figure shows the infra-cardiac sac of the right pleural cavity and the azygos lobe of the right lung lying within it.

Urinary Bladder.—It is a conical organ. The apex is prolonged into the urachus which stretches up on the inner surface of the abdominal wall. The base of the bladder or trigone has three openings which lie close together—these are the openings of the ureters and the urethral opening. The ureteric openings lie above the urethral opening which has a puckered margin. In the fresh specimen the musculature can be made out easily when the bladder is distended. There is a transverse bar of muscle tissue which stretches across between

the ureters. From the trigone, longitudinal fibres arise which converge on the apex of the urachus. The circular fibres are present. They lie internal to the longitudinal fibres and are continued into the trigone and into the urethra. In the female the flattening of the trigone is not so marked. The urethra is bound in this sex to the lower part of the uterus by fine areolar tissue. Lower down it is firmly attached to the anterior vaginal wall. It opens into the anterior part of the urogenital sinus. The disposition of the external parts of the female genitalia are described in the section on the external genitalia. The whole condition is very reminiscent of the *Tarsius* condition.

Male Genital Organs.

Scrotum.—The skin of the scrotum is free from hair but covered with minute raised whitish areas. Pocock has noted these as being present in all the members of the Hapalidæ. The skin is usually wrinkled in preserved specimens, but in the fresh specimens it is relatively smooth. In one animal, as has been noted above, the scrotum did not contain the testes. These had been retracted towards the external abdominal ring. It is possible that a dartos muscle is present, but this has not been confirmed microscopically. There is a covering of deep fascia common to the abdominal wall and the scrotum. The fascia forms the septum between the two sides of the scrotum. Separated from the deep fascia by loose areolar tissue is a tubular sheath of fascia from the external oblique muscle. This sheath is the external spermatic fascia. Deep to this is another tubular sheath covering the structures of the cord and the parietal coat of the tunica vaginalis. This sheath is derived from the transversus abdominus, and in it lie the fibres of the cremaster muscle, which are derived from the transversus abdominus. There is no demonstrable sheet from the internal oblique muscle. The tunica vaginalis is composed of a parietal and a visceral layer. The tunica extends a considerable distance towards the external abdominal ring. There is a digital fossa partly separating the testis from the epididymis. This fossa extends the whole length of the epididymis.

The Testis.—The testis is invested with a fibrous coat under the serous layer derived from the tunica vaginalis. This is the tunica albuginea. The arrangement of the fibrous structures and of the ducts is almost identical with that seen in the other Anthropoidea. The cells lining the ducts present the usual features. Fixation in the specimen sectioned was poor and the finer cytology of these cells was impossible to determine. They were identical with the cells of the human testis. Spermatogenesis seemed to be in abeyance and the spermatozoa seen were not normal. It is impossible to give a good account of these cells as the animal had been in captivity for some time before death and considerable endocrine changes had taken place.

Epididymis.—This is a large mass of tissue lying along the

medial border of the testis and is almost one-half the size of the testis. The tail is large and forms almost one-half of the epididymis. From the lower pole of the organ the vas deferens arises and runs along the medial side of the epididymis towards the external abdominal ring. It passes through the inguinal canal and reaches the abdomen. It passes over the brim of the pelvis and lying medially crosses over the ureter. It then gains the posterior surface of the prostate and lies medial to the vesiculæ seminales. It joins the duct of that organ to form the common ejaculatory duct and, passing forwards, it enters the prostatic urethra on the colliculus seminalis lateral to the medial depression in the centre of the colliculus. In its course to the urethra the common ejaculatory duct does not pass through the prostatic tissue but lies on the antero-superior surface of the gland.

Vesiculæ Seminales.—These are small and lie posterior to the prostate entirely within the pelvis. They measure about three millimetres long and two broad. They are filled with a yellowish glairy fluid. The sac is a simple one with a short duct opening into the vas deferens.

The microscopic structure of the other urogenital organs is identical with the condition found in *Tarsius*. Hence it is not proposed to describe the relations of the prostate and the structure of the erectile tissue of the penis.

Female Genital Organs.

Vagina.—The vagina is divided into two parts—one the superficial which is a mere antero-posterior slit, and a deep part which is almost cylindrical. Into the upper part of the deep portion the cervix of the uterus is invaginated. The rounded cervix projects vertically downwards, and on its most inferior part shows a slit-like os externum.

Uterus.—The uterus is best described as consisting of a cervix, a body, and a fundus. The cervix forms the lower fourth of the length of the uterus, the body the middle fourth, and the fundus the upper half. The uterus is very like the higher anthropoid uterus except for the fundus which is produced laterally into the tubal region. There is a median groove on the anterior surface of the upper part of the uterus which gives the impression that the lateral projection of the fundus is in reality a horn. The peritoneum is reflected from the uterus about the level of the lowest part of the fundus. Behind, the reflection extends below the level of the cervix on to the posterior wall of the vagina. The structure of the uterus has been worked out by Professor J. P. Hill.

Fallopian Tubes.—These are short straight tubes embedded in the broad ligament of the uterus. They terminate in single fimbriæ which lie along the inferior surface of the ovaries.

Ovaries.—They are the size of a small pea and are attached to the posterior layer of the broad ligament by a short mesovarium.

No corpora lutea were seen. No sign of Wolffian tubules were found in the broad ligament.

Broad Ligament.—The broad ligament stretches across from the lateral wall of the pelvis to the side of the uterus. Laterally and above it is continued into the ovarico-pelvic ligament in which run the ovarian vessels. The round ligament is present. The uterine artery passes along the side of the uterus and into the broad ligament to supply the Fallopian tube.

THE CENTRAL NERVOUS SYSTEM.

The central nervous system of *Hapale* has been investigated by Dr. H. H. Woollard, who is publishing at a later date a complete account of this system. Consequently I shall merely summarise the points which he has pointed out in his work. He has most generously allowed me to make use of this before publication so that this paper on the affinities of *Hapale* will be as complete as possible. The list of literature on the brain has been omitted from the bibliography at the end of this paper.

The brain of *Hapale* has been compared mainly with that of *Tarsius* and with a Mascarene Lemur.

Cerebral Cortex.—The cortex is smooth and shows only four fissures:—

1. The lateral fissure.
2. The superior temporal.
3. The calcarine.
4. The hippocampal.

In *Tarsius* a calcarine is present and possibly a faint suggestion of a pre-sylvian and a central.

The histological areas of the brain are well defined. The striate area is large and possesses a well-marked stria of Genarius. The piriform area is confined entirely to the base of the brain and the hippocampus is deeply buried. In *Tarsius*, on the other hand, the piriform area appears on the lateral surface of the brain, but much less than in the Lemurs where a large area is exposed. *Tarsius* has a well-defined area striata.

Commissures.—The corpus callosum of *Hapale* is large and possesses a genu and a rostrum and splenium. In *Tarsius* there is no genu or splenium. The ventral commissure is large in *Tarsius* and small in *Hapale*. The hippocampal commissure is small in both animals.

Mid-brain.—In a previous paper (1926) Woollard has described the relations and structure of the lateral geniculate body of both *Tarsius* and *Hapale*. In *Tarsius* the medial and lateral geniculate bodies lie more dorsal than in *Hapale*. The pulvinar in *Hapale* is much more prominent.

Woollard in this paper showed that with the development of a primordium maculæ luteæ there is a corresponding development of the lateral geniculate body. This increase in the lateral geniculate body affects the central part of

the dorsal nucleus. *Hapale*, which has developed a macula a stage further than *Tarsius*, has a corresponding greater development of the central part of the dorsal nucleus and a corresponding diminution in size of the reflex parts of the lateral geniculate body.

Cerebellum.—*Tarsius* differs from the Lemurs in that it does not possess a lobus paramedialis. In *Hapale* this lobe is absent. Bolk regards the cerebellum of *Hapale* as a very primitive structure and as the most primitive of all the monkeys. He regards the cerebellum of the Platyrrhinæ as the basal primate cerebellum, and of the animals belonging to this group he thinks that *Hapale* is undoubtedly the most primitive. He also states that the Primates are not developed from any living Prosimian, but that there is a close resemblance between the cerebellum of *Tarsius* and that of *Hapale*.

Pons.—*Tarsius* has a very primitive form of arrangement of the cells of the pons. The cells connected with the cerebro-pontine fibres are not numerous, while those connected with the formatio reticularis are at a maximum. In *Hapale* the cells connected with the cerebro-pontine fibres are more numerous and the cells of the ventral nucleus which are connected with the formatio reticularis have diminished.

SUMMARY AND DISCUSSION.

The summaries appended are intended to point out the close similarity of the general structure of *Hapale* with that of *Tarsius*. It is not proposed to draw general conclusions as to the exact place of the animal in the Primate family until a complete investigation has been made of several other Platyrrhinæ.

External Characters.

The animal is a small squirrel-like animal with large head and large flap-like ears. The flap is developed from the plica principalis as in *Tarsius* and indicates that the sense of hearing is well developed. On the face the tactile vibrissæ are well developed and arranged in a manner reminiscent of *Tarsius*. There is a carpal pad with a group of strong vibrissæ arising from it.

The tail is not prehensile, nor is there any trace in the specimens examined of scales with hairs projecting from beneath them as in *Ptilocercus*.

The pes and manus cannot be compared directly with those of *Tarsius*, as in that animal there is considerable specialisation of the foot and to a certain extent of the hand. When the pattern of the pads in the manus is compared with that found and described in *Ptilocercus* by Le Gros Clark, the similarity is very striking. There has been a fusion of pads distinct and separate in the latter animal to form larger areas in *Hapale*.

An examination of the arrangement of the epidermic ridges demonstrates that the basic pattern is identical in both. The fusion of the thenar and first interdigital pads in the pes has produced a condition only a stage more advanced than that in *Ptilocercus*. The pollex is not free in the sense that it can be apposed, but adduction and abduction although weak can be performed. The hallux is widely divergent from the remaining digits and bears a well-formed flattened nail. It can be adducted and abducted through a considerable range. It is used in exactly the same way as the hallux of *Cebus*, that is to obtain a grip on the tree-trunk in addition to the support obtained by the clinging claws which bite into the bark.

The face is flattened and the eyes look forwards, although the axes of the orbital cavity meet at an angle of 45 degrees and appear to face outwards as well as forwards. The nose is typical of the Platyrrhine group. The nostrils face outwards and slightly forwards.

The eyes do not appear to move much within their sockets during life; but this apparent absence of conjugate movements is compensated for by the great mobility of the head on the vertebral column, a condition like that in *Tarsius*.

The Skeleton.

In order that the outstanding characters of the skull may be readily compared with those of *Ptilocercus* and *Tarsius*, the following summary is arranged in the same order as the summary given by Le Gros Clark (1926) of the characters of the skull in *Ptilocercus*.

Primitive Features.

1. The premaxilla is small. It does not articulate with the frontal, and thus agrees with *Tarsius* and differs from *Ptilocercus*.
2. The malar though large does not extend backwards to the glenoid region as in *Ptilocercus*. It meets the lachrymal in front.
3. The lachrymal still possesses a facial portion, but this is very small.
4. The lateral position of the mastoid region and the extent of the petrous temporal on the base of the skull.
5. The basioccipital is short and wide.
6. There is an entotympanic bulla.
7. The nose is situated anterior to the brain-case. In this respect the condition is identical with that of *Tarsius*.
8. The organ of Jacobson is similar to that of *Tarsius* which is closely related to that in the Marsupials.

Lemurine Features.

1. The malar bone articulates with the frontal along the outer side of the orbit. It has a malar foramen which may be double.

2. The lachrymal foramen is situated immediately inside the orbital margin, or it may be regarded as marginal.
3. The orbital cavity faces outwards and forwards.
4. The supraorbital foramen is absent.
5. The orbits are large.
6. There is a large entotympanic bulla.
7. The auditory ossicles are intermediate between those of the Nycticeboid lemurs and the Cebidæ (*Doran*).
8. The venous sinuses of the skull resemble *Tarsius*.
9. The olfactory foramina are single as in *Tarsius*.
10. The nasal region is identical in its structure with that of *Tarsius*.
11. The tubular posterior nares are identical with *Tarsius*.

Anthropoid Features.

1. The face is considerably reduced.
2. The orbital cavity is almost completely closed off from the temporal fossa. The inferior orbital fissure although long is narrow.
3. The ethmoid forms part of the medial orbital wall.
4. The tympanic bone is ring-shaped, but is expanded internally to form the floor and wall and portion of the roof of the tympanic cavity.
5. The antero-internal portion of the bulla is not a single cavity but is made up of a number of small spaces. This is possibly a stage in the complete obliteration of this part of the bulla.
6. The internal carotid artery lies in the septum of the bulla and gives off no stapedia artery.
7. The ossicles of the ear approach the condition in the Cebidæ.
8. There is a notch in place of the supra-orbital foramen.
9. There are three nasal turbinate bones.
10. The cranial foramina are more anthropoid than in *Tarsius*. The foramen rotundum is separate. The superior orbital fissure is complete. The foramen ovale is composite and transmits a small middle meningeal artery in addition to the third division of the fifth nerve.

The Nasal Region.

The turbinal bones are three in number and are arranged as in *Tarsius*. The anterior portion of the nose in the dried skull is triangular and the posterior is tubular. The organ of Jacobson is similar in most respects to that of *Tarsius*. The absence of well-fixed material made it impossible to determine the exact histology of this area. The olfactory area is small.

The Orbital Cavity.

The walls of the orbital cavity are strikingly like those of *Tarsius*. The presphenoid forms a thin septum dividing off the

two cavities from each other. This septum is overlapped by the ethmoid in front and the orbital plate of the palate behind. On the lateral wall the frontal and malar have a wide articular margin. Below, the malar and the superior maxilla articulate for a considerable distance backwards, and hence there is formed a long infra-orbital canal. The inferior orbital fissure is narrow and in the recent state is covered over by a thin membrane continuous with the periosteum of the bones forming the boundaries of the fissure.

The optic foramen is large. The superior orbital fissure is large, and the great wing of the sphenoid forming its inferior boundary is carried laterally to articulate with the frontal. Within the orbital cavity two small foramina open into the posterior and lateral part of the wall; these transmit meningeal vessels from the ophthalmic artery. The foramen rotundum is separate from the superior orbital fissure and is displaced downwards so that it opens below the true orbital cavity. The orbital process of the palate is large.

Dentition.

The dentition of *Hapale* has been studied in such detail that it is unnecessary to detail it *in extenso*. The absence of the third molar differentiates the Hapalidæ from the other Platyrrhinæ. The teeth when studied in section (Carter 1921) demonstrate a structure of the enamel which in the opinion of Carter shows that there is some resemblance between that of *Hapale* and those of *Tarsius* and *Galago*. The structure of the dentinal tubules in *Hapale* is almost identical with that in *Callicebus*. Although in his paper Carter does not figure *Hapale*, the structure of the tooth in *Callicebus* figured in his paper may be taken as almost identical with that of *Hapale*.

Vertebral Column.

The number of vertebræ as far as the coccygeal region is the primitive number. Gregory is of the opinion that *Hapale* shows many features which link it closely to the arrangement and structure of the vertebræ of *Notharctus*. The close similarity to the *Tarsius* condition is very striking. *Hapale* has a much more primitive arrangement of the vertebræ than *Nyctipithecus*, which is regarded by Gregory as a much more primitive animal.

Appendicular Skeleton.

The shoulder-girdle presents many features of interest. The clavicle has a double bowing as in Man. The area for the pectoralis major (pars clavicularis) is large. The bone is strong and pushes back the lateral angle of the scapula to the mid-axillary line. The supra-spinous fossa is small and there is no supra-scapular notch. On the whole the girdle is very similar to that of *Tarsius*.

The humerus is longer relatively than in *Tarsius* and resembles that of *Cebus*. The proximal end is similar in structure to that of *Tarsius*, but the shaft has been lengthened, and with this increase in length the various ridges and elevations do not appear so prominent. There is no entepicondylar foramen. The articular surfaces on the inferior extremity of the bone are typical of the *Tarsius* condition. The radius and ulna are more bowed, and, if anything, are longer in proportion to the body-length than in *Tarsius*. The arm as a whole is longer than *Tarsius*. Supination and pronation are free movements. The distal extremities of the radius and ulna do not call for any remark.

The carpus contains an os centrale. The lunate articulates mainly with the os magnum. The scaphoid is separate. The pisiform is insinuated between the distal end of the ulna and the cuneiform.

The manus presents some difficulty. If Gregory's opinion is to be accepted as correct, the condition of the distal segment of the fore limb must be regarded as secondary and specialised. The arrangement of the carpal bones and the musculature of this portion of the limb approximate so closely to the very primitive condition described by Le Gros Clark in *Ptilocercus* that it would be dangerous to accept this statement without reserve. It is more likely that *Hapale* is more primitive than has been thought, and there has not been any specialisation in the fore limb in the direction of the typical Primate manus. It is hard to conceive that *Hapale* specialised in the direction of flattened nails and expanded terminal phalanges, and then dropped these undoubtedly specialised features to return to a condition which approximates closely to that seen in some of the most primitive of the Insectivora, animals which have so many affinities to the *Metatheria*. It is more likely that *Hapale* derived the present sharp clinging claw at a very early stage in its history from claws similar to those of an animal like *Ptilocercus*. The pollex has become a simple digit although its musculature still remains well defined.

The hind limb as far as the ankle bears close resemblance to *Tarsius*. Muscles which were specialised for leaping in *Tarsius* remain in a primitive condition. The extensors and the adductors in the thigh are much smaller than those in *Tarsius*. The caudo-femoralis is present in its primitive state. In the pes the design of the tarsus is identical in the main features with that of *Ptilocercus*. The great development of the flexor muscles is correlated with the clinging habit. The hallux has become abducted from the side of the pes, but its head is still attached to the body of the pes by a strong ligament attached to the head of the second metatarsal. Thus it is only the terminal or phalangeal portion of the hallux which is free. The metatarsal has a limited range of movement, but it can be rotated on the entocuneiform to some extent. The pes appears to have

specialised from a primitive insectivorous condition only in that the hallux has become feebly opposable. There is no evidence to suppose that *Hapale* ever had a flattened nail or flattened terminal phalanges on its pes. The metatarsals have become elongated secondarily from the primitive condition, but this appears to be due to the retention of a plantigrade method of progression in addition to the clinging habits when at rest. Abduction and adduction of the metatarsals can be effected to give the animal a wider base of support when at rest.

Central Nervous System.

To summarise the conclusions reached by Dr. Woollard on this system, it may be said that *Hapale* is a stage further on in the direction of the more specialised higher Primate brain. It bears many resemblances to the brain of *Tarsius*. The visual apparatus has become more specialised in conjunction with the acquisition of a macula lutea of the eye. Generally speaking, it is the most primitive brain of all the Primates, with the exception of the Prosimiæ including *Tarsius*.

The brain of *Hapale* weighs one twenty-ninth of the body-weight of the animal (Hrdlička). It is therefore the largest-brained of all the Primates in proportion to body-weight.

Blood-Vascular System.

The heart is much more transverse than that organ in *Tarsius*. The pericardium is separated off from the diaphragm by a small infra-cardiac recess, but at the apex of the ventricles the pericardium is fused with the upper surface of the diaphragm. The great vessels arise in the typical primate manner. The vertebral arteries are large. The internal carotid arteries do not separate off from the common stem until above the level of the great cornu of the hyoid bone. The arrangement of the internal carotid artery within the skull is more advanced than in *Tarsius*. The stapelial artery is absent.

The limb vessels are arranged in a primitive manner.

Digestive System.

The tongue has been discussed in the section on the digestive system. It has a tip which is covered with fungiform papillæ. The intestinal tract is a more complicated structure than that in *Tarsius*. The stomach is simple, but histological examination shows that there is a distinct difference between the arrangement of the glands at the cardia from those at the pyloric end. The small intestine is arranged in six small coils or loops, each of which receives a large branch from the superior mesenteric artery. The terminal ileum passes downwards along the medial edge of the ascending colon, and turning upwards joins the large intestine at a distinct angle. The large intestine forms a complete oval loop which surrounds the small intestine. The cæcum, which is wide and ends at a blunt hooked extremity, normally lies in the

false pelvis. The ascending colon ascends along the right side of the abdomen as far as the inferior surface of the liver and then becomes transverse in its course. The splenic flexure is present, and sometimes it is possible to identify an incipient pelvis loop. The rectum is perfectly straight. The gut is simple in its mesenteric connections. Rotation has progressed to the same extent as seen in Man. The transverse mesocolon is not fused to the under surface of the great omentum.

The liver resembles the condition in *Nycticebus* and is lodged almost entirely under cover of the ribs. The caudate lobe is large. The mesenteric attachments are simple and there is no bare area. The gall-bladder lies to the right of the middle line along the inferior surface of the right central lobe. The umbilical fissure is well marked.

In general, the gut of *Hapale* presents an elaboration of the primitive condition seen in *Ptilocercus* and *Tarsius*. The length of the tube is greater in proportion to the body-length in *Hapale* than in *Tarsius*. The liver is lemurine, and the primitive arrangement of fissures and lobes is retained.

Urogenital System.

The urogenital system in the male has many features of interest. The testes in two fully-grown animals which had not been injected and which were received immediately after death, were retracted up into the inguinal fold and their upper poles were inserted into the external abdominal ring. Normally they lie within the scrotal sacs. The penis is buried in the mass of tissue which overlies the upper part of the pubic area. When everted it is seen that there is a faint suggestion of a frenum. The prepuce is not visible as a free fold of skin. The scrotal sacs are composed of the same layers as in Man, except that it is not possible to demonstrate the presence of a dartos muscle under the skin. The cremaster is derived mainly from the internal oblique.

The musculature and the prostate are arranged as in Man. The seminal vesicles are smooth in some animals, but in others they are seen to be covered with small sacculations. On section these are seen to open freely into the general cavity of the vesicle. The vas deferens unites with the duct from the seminal vesicle to form a single common ejaculatory duct for each side.

The female has a urethra which opens independently of the vagina. The urinary opening is situated anterior to the vaginal aperture as in the human subject. The uterus is single, but there is a suggestion of a double uterus in some young animals caused by a shallow groove on the anterior surface of the body of the vagina. On section the uterus is seen to be single. The animal produces twins at a birth and sometimes triplets.

The embryology of the animal is being worked out by Professor J. P. Hill. The animal has been bred successfully in captivity. (Lucas, 1927.)

Respiratory System.

The structure of the larynx is interesting in that it presents many primitive features and because of its close resemblance to *Tarsius* on one hand and the less specialised members of the Cebidæ on the other. The lungs are less complex than in *Tarsius*. On the right side there are four lobes and on the left only two. There is an azygos lobe on the right side. The pulmonary veins are arranged in a peculiar manner. On the right side all the lobar veins unite to form a single trunk which enters the left auricle. On the left side the veins from each lobe do not unite, but enter the auricle separately. In this way *Hapale* is a stage more advanced than *Tarsius*, where there are only two pulmonary veins, one from each lung.

The rings of the trachea are broad, and there is a very thin membrane between them. They lie close together, and are incomplete behind.

Myology.

I do not wish to set out in any detail the conditions described in *Hapale* and compare them with the other Platyrrhinæ until I have had an opportunity to investigate these animals more closely. In general, it is possible to state that *Hapale* demonstrates an exceedingly primitive type of musculature more primitive in many ways than that of *Tarsius*, but similar to that animal in so far as they both approach the primitive insectivore condition.

GENERAL CONCLUSIONS.

Hapale in the form of its brain and the changes which have taken place in its special sense organs presents a stage in the evolution of the Primates more advanced than that seen in *Tarsius*. These advanced characters are associated with the retention of many primitive features in its general anatomy. There is not sufficient evidence to justify the conclusion of Gregory that the manus and pes of *Hapale* are specialised structures. On the other hand, there is ample evidence, as presented by an investigation of the bony structures of the foot, to justify the conclusion that *Hapale* still retains the primitive manus and pes almost unaltered from the primitive insectivorous condition seen in *Ptilocercus*.

In other ways the animal shows signs of specialisation in the direction of the higher Primates. The arrangement of the lungs, the tendency to simplification of the lobes and the vascular connections, are more advanced than that seen in *Tarsius*. The digestive system, in many ways primitive, is more like that in some of the Cebidæ than in the Lemurs. On the other hand, the form of the liver is still lemurine.

The similarity in the structure of the skull of *Hapale* and *Tarsius* can only be appreciated either by a close study of the

two animals or by comparing the account given by Woollard with the account above. The striking similarity of the nasal region, the orbital cavity, the structure of the vertebral column, and the proximal segments of the limbs are too close to deny that there is no close relationship between these two animals.

If *Tarsius* is regarded as "standing at the base of the Primate stem" and reaching "forth to the Simian forms," then *Hapale* is but a modification of the Tarsioid ancestor leading upwards towards the Platyrrhinæ and is itself the most primitive and tarsioid of these forms. When the fossil record of the Platyrrhinæ becomes better known, it will connect up the Eocene Tarsioids with the recent Platyrrhinæ, and it is possible that one of the stages in the phylogeny of the group will closely resemble the living Hapalidæ.

The absence of the third molar is, as has been pointed out above, but the logical conclusion to the retrogressive form of this tooth throughout the whole of the primitive Primates. There will be found, there is little doubt, forms which present all the stages between the fossil Tarsioids and the living Hapalidæ.

The general conclusion may be summarised thus:—*Tarsius* has specialised in the direction of the higher Primates and also for a particular mode of progression. *Hapale* has retained a primitive method of progression with a more highly specialised Primate brain. There is little doubt that there is every reason for separating off the Hapalidæ from the Platyrrhinæ as Huxley did, and for regarding them as the most primitive of all the living monkeys.

Whether the Hapalidæ throw any light on the origin of the Old World Monkeys and the Anthropoidea must remain undecided until a more critical study is made of members of these groups. It is better to regard the Hapalidæ as the living survivors of a stage in the evolution of the Platyrrhinæ and as closely related to the ancestors of the living *Tarsius* and the fossil Eocene Tarsioids.

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EXPLANATION OF THE PLATES.

PLATE I.

The Skeleton.

PLATE II.

Photomicrographs of hairs: (a) *Hapale*, (b) *Galago*, (c) *Tarsius*. $\times 500$.

39. The Gibbons of the Genus *Hylobates*.

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(Text-figures 19-23.)

The Gibbons of the genus *Hylobates* exhibit, within specific and subspecific limits, individual variation of colour surpassing, I believe, that of any other species of mammals. This variability, totally unsuspected, naturally led to the description of a number of spurious species, of which most of the names have long been consigned to the category of synonyms. But even at the present time, owing partly to inappreciation of the affinities of the existing forms, partly to differences in the modern interpretation of the term "species," there seems to be no sort of agreement amongst systematists as to the number of groups of that rank to be admitted. Formerly some six or seven were generally regarded as valid; but Matschie admitted thirteen, and in the latest monograph, namely Elliot's Review of the Primates (III.), pp. 149-175, 1913, as many as twelve are enumerated, although the status of a few of them is regarded as doubtful.

The British Museum contains a good collection of skins and skulls of the genus; and study of this material has convinced me that there are only three definable species as I understand that term. It is not, however, my purpose to give a complete synonymical catalogue of the group. All that I propose in this paper is to justify as far as possible the reduction above mentioned in the number of species, and to give my reasons for dissenting from my predecessors in a few questions concerned with nomenclature and other matters.

One conclusion of general zoological interest that has emerged from the work, but has not, I think, been previously apprehended, is the absence of secondary sexual characters in the genus. There may be, it is true, in some cases, differences in colour between adult males and females; but I can find no reliable instance of differences between them in size and strength of body, skull, or teeth. In this respect Gibbons depart very strikingly from the rest of the Catarrhine Primates, and more particularly from their nearest allies, the Gorilla, Chimpanzee, and Orang Utan, than from some of the smaller monkeys. This sexual similarity I believe to be a secondarily acquired character; and I find in it an item of evidence in favour of the view I long ago published that the existing Gibbons are dwarfed Anthropomorphs, dwarfed in the interests of their unique arboreal activities to which weight would be a serious disadvantage.

The external characters distinguishing the three species above referred to may be tabulated as follows:—

- | | |
|--|------------------|
| a. Crown of the head comparatively flat owing to the generally horizontal direction of the growth of the hairs; a pale brow-band; postero-inferior portion of the rim of the ear not confluent with the skin of the head; clitoris comparatively short, not grooved below. | |
| b. Rump, including the nearly naked skin round the anus, the callosities and the genitalia more naked and exposed, not concealed to so great an extent by the hairs of the surrounding areas; preputial tuft in males much smaller | <i>lar.</i> |
| b'. The above-mentioned areas not so naked and concealed to a much greater extent by the surrounding hairs; preputial tuft larger, in fully adult or old males very long and beard-like | <i>hoolock.</i> |
| a'. Crown of head not flat, the hairs upstanding and forming in the adult a thick crest or mat; no pale brow-band; postero-inferior portion of rim of ear confluent with the skin of the head; clitoris very long and grooved throughout beneath | <i>concolor.</i> |

The three may be briefly distinguished as follows by their cranial characters:—

- | | |
|---|------------------|
| a. Interorbital septum inclined at a tolerably steep angle to the forehead, the thickened upper edges of the orbits extending across the middle line. | |
| b. Smaller; orbits relatively wider, inner ends of brow-ridges more strongly developed; facial portion of skull lower; maxillæ weaker and teeth smaller | <i>lar.</i> |
| b'. Larger; orbits relatively narrower, inner ends of brow-ridges less strongly developed; facial portion of skull higher; jaws more massive, teeth larger | <i>hoolock.</i> |
| b. Interorbital septum forming a continuous slope with the forehead above and nasals below; the brow-ridges not extending across the middle line; facial portion of skull low and relatively narrow across the orbits | <i>concolor.</i> |

From these tables it appears that *H. lar* and *H. hoolock* are more closely related to one another than either is to *H. concolor*. Nevertheless *H. lar* and *H. hoolock* cannot on the available evidence be assigned to the same species. In addition to the characters mentioned above they differ in voice. Moreover, according to Anderson they occur together in some parts of Burma, *i.e.* Arakan, presumably without blending (*cf.* however below, p. 733).

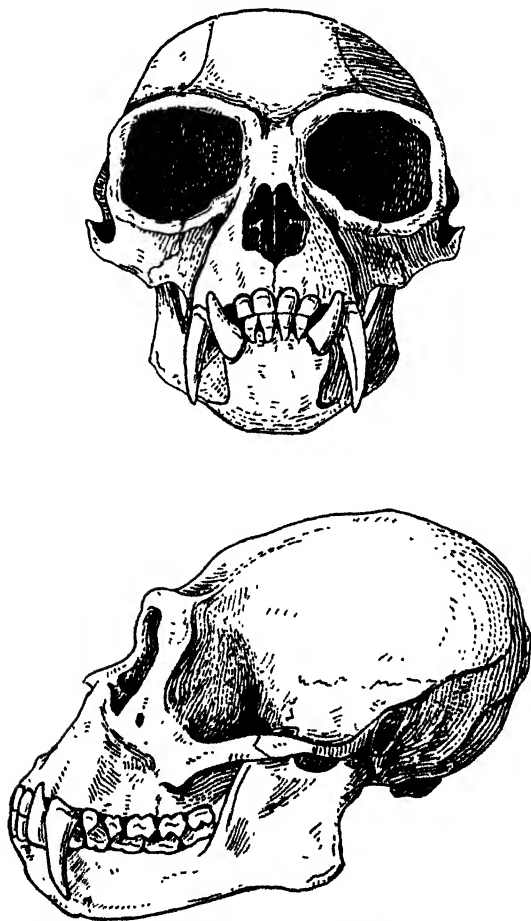
HYLOBATES LAR Linn.

Colour, as described under the subspecific headings, exceedingly variable, and ranging from nearly black all over to uniformly pale fawn.

Skull with comparatively low facial region, weak maxillæ, and small teeth, but broad across the orbits, with brow-ridges strongly developed; more noticeably so towards the middle line than in the other species, the interorbital area forming a marked angle with the frontal region above and with the nasals below, these bones typically horizontal or nearly so and giving a characteristically "snub-nosed" appearance to the face. (Text-fig. 19, p. 721.)

The clitoris small and ungrooved as in *H. hoolock*, not long and grooved beneath as in *H. concolor*; the buttocks less overgrown with hair, and the preputial tuft of the male smaller than in *H. hoolock*. The ear, as in the latter, not confluent at the base behind with the side of the head as in *H. concolor*.

Text-figure 19.



Skull of *Hylobates lar lar*, ad. ♂, from Bankachon, Tenasserim.
¾ nat. size.

Distribution. From Lower Burma and the adjoining areas of Siam and Cambodia southwards into the Malay Peninsula and thence through Sumatra and Java to Borneo and the Sulu Islands.

Anderson long ago stated that he could perceive no cranial differences between the five forms *lar*, *pileatus*, *agilis*, *leuciscus*, and *mulleri* which by most authors have been hitherto cited as valid species. Since my observations bear out Anderson's statement, I regard the Gibbons so named merely as subspecies of *lar*, the first form of the group to receive a name, the differences in colour between them being, in my opinion, too unimportant to be granted specific value.

Some of the differences in colour between these subspecies are summarised in the following analytical key:—

- a. At least the distal portions of the hands and feet, with the fingers and toes, white, and particularly conspicuously contrasted with the arms and legs in the black phase.
- b. Typically, but not invariably, the wrists and ankles, as well as the hands and feet, wholly white; face more constantly encircled with white, but never a white stripe on the occiput defining a dark patch on the crown; pale phase without black on the crown or on the lower side and cheeks; genital hairs not contrasted in the dark phase, only in the pale phase, in which they are brown *lar*.
- b'. Wrists and ankles and tops of hands and feet never so white; white facial area sometimes restricted to the brow-band; generally a white band on the occiput defining a black patch on the crown in front; pale phase generally with a dusky or black crown, frequently accompanied by a black shield on the chest and abdomen, and sometimes with black cheeks as well; genital hairs conspicuously white in the black phase in the male, pale, not brown, in the pale phase *pileatus*.
- a'. The hands and feet, fingers and toes approximately the same colour as the arms and legs respectively.
- c. A black, or nearly black, and a pale buffy-white phase, with intermediates between them, occurring as in *lar* and *pileatus*; the black phase with the posterior half of the back and the loins deep brown; no differentiated dark crown *agilis*.
- c'. No black or pale buffy-white phases, the range in colour less extensive; summit of the head darkened as in typical forms of *pileatus*, and the cheeks, throat, ventral surface and inner side of arms and legs very often darker than the back; hairs round the genitalia black or brown, darker than the surrounding area and never forming a conspicuous tuft in the male.
- d. Colour typically slate-grey, clouded to a greater or lesser extent with brown; ventral surface not darker than dorsal *leuciscus*.
- d'. Colour browner above, the ventral surface and inner side of limbs typically darker than the dorsal *mulleri*.

Subspecies *LAR* Linn.

Homo lar Linnæus, Mantiss Plant., App. p. 521, 1771; and of all recent authors under *Hylobates*.

Colour ranging, irrespective of sex, from black through various shades of brown to buff or almost cream, pale forms predominating. A paler ring encircling the face, and the hands and feet typically white from the wrist and ankles to the tips of the fingers and toes. The facial ring, however, varies considerably in width and, in the black phase, the wrists and ankles are sometimes black, the blackness very occasionally extending some distance along the top of the hands and feet. In the black

phase the back is occasionally grizzled behind the shoulders, but the genital tuft in the male is black and there is no white line passing from the ear on to the occiput. In the pale phase also there is no differentiated dark patch on the crown, and the ventral surface is pale.

Distribution. Arakan and adjoining districts of Lower Burma (according to Anderson); Tenasserim and the adjoining districts of Siam southwards into the Malay Peninsula. I have seen no examples of this race procured north of Tenasserim.

The following are the approximate measurements, in inches, of a few selected large examples:—

Locality.	Sex.	Head and Body.	Hind Foot.
Tenasserim	♀	22½	6+
"	♂	22	6—
"	♂	20	6+
Chong Trang, Siam. . .	♀	21+	5½+
Um Pang, Siam	♂	20+	6—
Pahang, Malaya		22+	5½

The average size is smaller than indicated by the examples measured, the length of the head and body being more often than not under 20 inches. The weight is from about 12 lbs. to 15 lbs.

Some skull-measurements, in mm., are as follows:—

Locality.	Sex.	Total length.	Basal length.	Lg. of Palate.	Lg. of Upper Molars.	Orbital width.	Zygomatic width.
Tenasserim	♂	110	79	37	27	66	73
"	♀	109	78	38	27	66	74
"	♀	108	77	36	26	66	71
"	♂	106	77	37	26	66	73
"	♂	97	69	33	23	66	70

The British Museum has a very fine series of this Gibbon. Those from Tenasserim were obtained by the collectors of the Mammal Survey of British India, carried out by the Bombay Natural History Society, and those from the Malay Peninsula by Messrs. H. C. Robinson and C. Boden Kloss.

Special attention may be drawn to two black males from Tenasserim which, in having the wrists and ankles black and the upper sides of the feet and to a less extent of the hands markedly infuscate, link in this respect typical *H. lar lar* with the next form, *H. lar pileatus*.

Subspecies PILEATUS Gray.

Hylobates pileatus Gray, Proc. Zool. Soc. Lond. 1861, p. 136, pl. xxi.; and of subsequent authors.

Hylobates lar pileatus C. B. Kloss, Proc. Zool. Soc. 1916, pp. 29-30.

Resembling *H. lar lar* in presenting several colour-phases. The black phase with the hands and feet not so white as in typical *lar*, the black from the wrist and ankle spreading more or less and with varying intensity on to their upper sides and on the foot even to the base of the toes, a variation only of occasional occurrence in *H. lar lar*; the face sometimes surrounded with a white band, as in typical *H. lar lar*, sometimes the white band restricted to the forehead; the crown of the head sometimes practically wholly black, sometimes with a more or less conspicuous greyish stripe passing from the ears on to the occiput and defining posteriorly a black triangular patch. Intergrading with *H. lar lar* in the above-mentioned characters, but always distinguishable from it by the tuft of hair round the penis being white and very conspicuous instead of black.

The pale phase typically differs from the similar phase in *H. lar lar* in having a blackish area on the crown of the head and a large black area at least on the lower part of the chest and on the abdomen; but sometimes in this phase the whole chest, the throat and the cheeks are also black. The type-specimen itself is intermediate between the black and pale phases, the back being brown instead of black. The palest of all the available specimens are a young individual in which the general pallid hue of the pelage is merely relieved by a dusky patch on the head and an entirely pale adult female.

Distribution. S.E. Siam and Cambodia.

In addition to the type above referred to, which came from Cambodia, the British Museum possesses several good specimens of this race collected by Mr. C. Boden Kloss in S.E. Siam, two adults and one young male from Klong Menao and an adult female from Lem Ngap. One of the adult males has the black patch on the crown practically undefined posteriorly by a grey band, and can be scarcely distinguished from an example of *H. lar lar* from Tenasserim, which has the upper side of the hands and feet blackish-grey, except by the whiteness of the hair-tuft on the penis. The adult female differs from most of the pale examples previously recorded in having the cheeks, throat, and fore part of the chest black, as well as the crown of the head, the belly, and the posterior area of the chest.

The young male is the pale specimen, with the dusky crown-patch, above referred to. This specimen is of interest because its coloration is practically the same as that of adult female examples of *H. concolor* inhabiting the adjoining districts of Laos and Tonkin; and in connection with this resemblance it may be

recalled that a female of *concolor* from Hainan, when changing colour, passed through a phase resembling typical pale examples of *H. lar pileatus* in exhibiting a black patch on the chest and belly and on the crown.

So far as I am aware, Mr. C. B. Kloss was the first author to state that *H. pileatus* is only a subspecies of *H. lar* (Proc. Zool. Soc. 1916, pp. 29-30). I came independently to the same conclusion before reading Mr. Kloss's remarks.

The measurements, in inches, of three adults taken in the flesh by Mr. C. B. Kloss are as follows:—

Locality.	Sex.	Head and Body.	Hind Foot.
Klong Menao, S.E. Siam	♂	19½—	6+
" "	♂	18½+	6
Lem Ngop, S.E. Siam...	♀	18½+	6—

Some skull-measurements, in mm., are as follows:—

Locality.	Sex.	Total length.	Basal length.	Lg. of Palate.	Lg. of Upper Molars.	Orbital width.	Zygomatic width.
Klong Menao ..	♂	105	73	35	23	62	74
"	♂	102	73	36	26	63	68
Lem Ngop ...	♀	100	70	33	25	63	67
Cambodia (type).	♂	98	...	37	24	63	75

Although somewhat meagre, these dimensional data suggest that *H. lar pileatus* is a somewhat smaller race than *H. lar lar*.

Subspecies *AGILIS* Cuv.

Hylobates agilis F. Cuvier, Hist. Nat. Mamm. pls. v. & vi. 1821; and of subsequent authors.

Distinguishable from *H. lar lar* and *H. lar pileatus* by having the hands and fingers, the feet and toes wholly black in the black phase and approximately the same colour as the arms and legs in the pale phase. Also in the black phase the back is chocolate-brown, somewhat paler on the loins and rump. Other colour-characters variable. The dark and pale phases and intermediates, between them, exist as in *H. lar lar*. The amount of white round the face in the dark phase is more variable than in *H. lar lar* and resembles that of *H. lar pileatus*, sometimes involving the throat, cheeks, and brow, sometimes existing only on the brow, where it may be represented by a very narrow band. Black individuals with a white brow-band are very like examples of *H. hollock* except for the brown tinge of the loins and hips, the more naked rump, and the inconspicuous preputial tuft in the adult male.

The British Museum has a tolerably good series of skins of this race. The following particulars illustrate their variability in colour :—

1. ♂. Taiping, Perak. Deep brown on back, becoming paler chocolate-brown on loins, rump, and upper part of thighs; ventral surface and limbs black, but throat browner than chest, whiskers dirty white, and a broad whitish brow-band.
2. ♂. Batu Tejor, Perak. Differing from No. 1 in having the whiskers deep brown, like the neck and head (?); a well-defined brow-band.
3. ♀. Maxwell Hill, Taiping, Perak. Like No. 2.
4. ♀. Tanjong Hantu, Dindings. Like No. 2, but the brow-band is much less distinct.
5. ♂. Kedah. Very like No. 1.
6. Malacca. Very like No. 4.
7. ♀. Sumatra. Very like No. 1, but cheeks brown.
8. ♀. Pisang (? Padang), Sumatra. Like No. 1, but with throat as well as cheeks and brow dirty white.
9. Sumatra. Intermediate in tint between the dark and light phases.
10. Sumatra. Pale phase, cream or whitish-buff all over.

The following approximate measurements in inches are taken from skins collected by Messrs. H. C. Robinson and C. Boden Kloss in the Malay Peninsula :—

Locality.	Sex.	Head and Body.	Hind Foot.
Taiping, Perak	♂	19½	5½ +
Batu Tijor, Perak .. .	♂	19 +	5½
Tanjong antu, Perak	♀	18½—	5
Taiping, Perak	♀	19½—	5—

The measurements, in millimetres, of some adult skulls are as follows :—

Locality.	Sex.	Total length.	Basal length.	Lg. of Palate.	Lg. of Upper Molars.	Orbital width.	Zygomatic width.
Sumatra	108	77	38	26	63	71
Perak	♂	106	75	36	26	61	66
"	♂	103	74	35	27	68	70—
"	♀	99	74	36	25	62	65
"	♀	104	70	35	25	58	66
Kedah, Sumatra .	♂	101	74	35	25	66	68

The four skulls from Perak belong to the skins recorded above, and are enlisted in the same order.

The average dimensions both of the skins and skulls are in tolerably close agreement with those of *lar* and *pileatus*.

Subspecies *LEUCISCUS* Geoffr.

Hylobates leuciscus Geoffroy, Ann. du Mus. xix. p. 89 *; and of subsequent authors.

Distinguishable from the three preceding subspecies of *Hylobates lar* by the general colour being tolerably uniformly grey and subject to less individual variation, there being no pronounced black and buff phases; but resembling *agilis* in having the hands and feet the same tint as the arms and legs, and the dorsal area at least sometimes paler posteriorly than anteriorly. The face is surrounded by paler hairs on the brow, cheeks, and throat as in some specimens, at all events, of *lar*, *pileatus*, and *agilis*, and, as in some specimens of *pileatus*, there is a darker patch on the head. The hairs round the genital area, at least in the male, are deep brown, and show up as a conspicuous patch against the paler surrounding area.

Distribution. Java.

According to Anderson and, following him, Forbes (Handb. of the Primates, II. p. 155), who was personally acquainted with the Gibbon in Java, the coat is thick and woolly and the general colour is ashy-grey, paler on the lower back and rump: the top of the head is black with a white superciliary streak, and the hair round the face is grey.

This race is poorly represented in the British Museum, the only adult example being a male collected by G. C. Shortridge at Preanger, 4000 feet, in Java. This specimen differs in some details from Forbes's description. The general colour above is slaty-grey, clouded with brown, but the back is not appreciably paler behind than in front. The top of the head is brownish-grey, blending on the neck with the paler slaty-grey hue of the back, and sharply defined in front by a clear grey brow-band, which passes into the rather darker grey hue covering the cheeks as far back as the ears and the throat to the larynx. The shoulders in front are browner than the back; but the chest is somewhat paler than the back, showing patches of dirty white. The preputial hair is black and conspicuous.

Two half-grown specimens from the same locality in Java are similar to the adult, but are a shade browner on the limbs and have more dirty white below.

The approximate measurements, in inches, of the only adult of which the dimensions are recorded are as follows:—

Locality.	Sex.	Head and Body.	Hind Foot.	Ear.
Preanger, 4000 feet ...	♂	25	6	1½—

* Owing to an error by Wagner the name *leuciscus*, as Elliot pointed out, was ascribed by Anderson and others to Schreber, 1775.

The length of the head and body of this specimen suggests that this Javan race may attain a greater size than the other subspecies of *H. lar*; but since only a single specimen is available for comparison, no definite conclusion can as yet be drawn from the data.

Subspecies *MULLERI* Martin.

Hylobates concolor Müller, Verh. Ges. p. 48, 1841; and of Anderson, Forbes, Elliot, and others (not *concolor* Harlan).

Hylobates mulleri Martin, Hist. of Quadrupeds, p. 444, 1840; Hose, Mammals of Borneo, p. 6, 1893.

Intergrading with *H. lar leuciscus*, and resembling it in having the hands and feet the same or nearly the same tint as the arms and legs, in the dark hue of the genital patch, and in the absence of the pale buff and black phases; but differing in the general tint of the dorsal surface being browner, without the slate-grey tinge, and the ventral surface usually darker than the dorsal.

Locality. Borneo and the Sulu Archipelago.

The British Museum has a good series of skins of this Gibbon collected mostly by Mr. C. Hose and Messrs. Robinson and Kloss. Judging from these, *H. lar mulleri* is more variable in colour than *H. lar leuciscus*; but the available material of the latter is too scanty at present to justify insistence on this point.

The following notes upon some of the specimens will illustrate the range in colour :-

Adult male from Paku, S.W. Sarawak (*H. C. Robinson*). Very like the adult male of *H. lar leuciscus* from Preanger, in Java, with the ventral surface pale, but the dorsal surface and the legs a paler, more buffy grey, without slaty tint. A second male from the same locality is much browner.

A young female from the Baram River (*C. Hose*) is also similar to the Javan specimen, but is browner and less slate-grey above.

These specimens with the pale ventral surface are intermediate between the Javan specimens and the typical Bornean specimens, which are darker below than above. A few of these may be noted.

An adult male from Anyut Saribas, S. Borneo (*Robinson & Kloss*), has the top of head black, fading into brown on the nape and set off by a grey brow-band; whiskers greyish-brown; nape, top of shoulders, arms and hands, and fore part of back deep brown, fading posteriorly on the rump and legs to pale sepia-brown; front of shoulders, fore-part of chest, and sides of neck black like the top of the head; hind part of chest greyish, clouded with black, passing into greyish on belly. An adult female from the same locality is like the male, but is paler on the head, shoulders, and sides of neck, which are brown, not black; the anterior portion of the back is also paler. An adult female from Betong Saribas, Sarawak, is a little paler above than the preceding, but the cheeks and throat are dusky brown, there is scarcely a trace of the pale brow-band, the feet are paler

than the legs, and the whole of the ventral surface and the insides of the limbs are black. But an immature female from the same locality is nearly uniformly greyish or buffy brown on the shoulders and fore part of the back and paler buff on the loins, rump, legs, lower half of the arms, and on the belly, chest, and whiskers; the head has a pale brow-band, but the dark patch on the crown is hardly differentiated.

A large adult female from Gunong Sidong, Samarahan, 1200 feet, has dark cheeks like the adult female from Betong Saribas, but there is a distinct whitish brow-band, and the throat, chest, belly, and inside of the limbs are brownish, not black.

In a series from the Baram River (*C. Hose*) one adult male is as pale on the ventral as on the dorsal surface, as in *leuciscus*; but the rest have the cheeks, the sides of the neck, the whole of the ventral surface, and the inside of the arms and of the legs to the knee blackish-brown, the front of the shoulders and the throat being blacker; the dorsal surface is golden or buffy brown from the occiput to the base of the thighs, the outside of the arms and legs brown, the top of the head blackish, and the brow-band greyish. These specimens vary in tint, some being lighter some darker both above and below; but the lower side is always darker than the upper, except in the one adult male, which is exceptional in this respect.

An adult from Mt. Kina Balu resembles the series from Baram in a general way, but has a shaggier coat, and the black on the inner side of the arms and legs is much more sharply defined, forming a long band or stripe.

The approximate dimensions, in inches, of some specimens measured by Messrs. H. C. Robinson and Boden Kloss are as follows:—

Locality.	Sex.	Head and Body.	Hind Foot.	Ear.
Samarahan	♀	22+	6½—	1½+
Anyut Saribas ...	♂	19½	5½	1½—
Betong Saribas....	♀	19+	5½	1½+
Anyut Saribas ...	♂	19	6	1½
" "	♀	19	5	...

The following are some measurements, in millimetres, of skulls obtained by the same collectors:—

Locality.	Sex.	Total length.	Basal length.	Lg. of Palate.	Lg. of Upper Molars.	Orbital width.	Zygomatic width.
Samarahan ...	♀	108	79	41	26	68	71
Anyut Saribas ...	♂	109	75	37	25	65	69
" " ...	♂	104	75	37	...	67	71
Paku, S. Sarawak	♂	104	74	37	25	62	70
Anyut Saribas ...	♀	102	71	36	28	62	64

HYLOBATES HOOLOCK Harl.

Simia hoolock Harlan, Tr. Amer. Phil. Soc. iv. p. 52, pl. 2, 1834; and of most subsequent authors under *Hylobates*.

Hylobates fuscus Winslow Lewis, Journ. Nat. Hist. Soc. Boston, i. pt. 1. p. 32, pls. 1 & 2, 1834.

Hylobates choromandus Ogilby, Proc. Zool. Soc. 1837, p. 689.

Hylobates scyritus Ogilby, Royle's Illustr. Him. Bot. p. lx, 1839.

Exhibiting two well-marked colour-phases, the darker and the lighter, which, however, do not appear to intergrade, both being subject to comparatively slight individual variations.

In the dark phase the entire pelage is black, sometimes tinged with brown on the shoulders and ventral surface; but the blackness of the head is always relieved by a wide white or whitish-buff brow-band, which may be entire or mesially interrupted, and there is not infrequently a patch of the same hue behind the chin, which may extend up the sides of the cheeks to the brow-band completely encircling the face. The genital hairs are black, greyish or reddish buff.

The pale phase is more variable. The whole of the upper surface and the outer and inner surfaces of the limbs may be a tolerably uniform golden or ruddy buff, or brownish buff clouded with brown on the back, or buffy-white on the head, nape, fore part of the back, shoulders, and arms, becoming clouded with brown on the flanks and loins and legs; the hands and feet may be the same tint as the arms and legs, but usually the digits, or at least their distal ends, are black. The brow-band is always whitish, but is only sharply defined when the crown behind it is brownish or buff, and the face is partially or wholly encircled with whitish hairs, which generally spread inwards beneath the eyes. The whole of the ventral surface, at least in the middle line of the throat, and the cheeks up to the ears are a darker or lighter brown, always darker than the dorsal surface, and the brown hue of the cheeks, often very dark, emphasises the pale rim round the face. The genital hairs are a paler or deeper brown or almost black, and always darker than the surrounding areas.

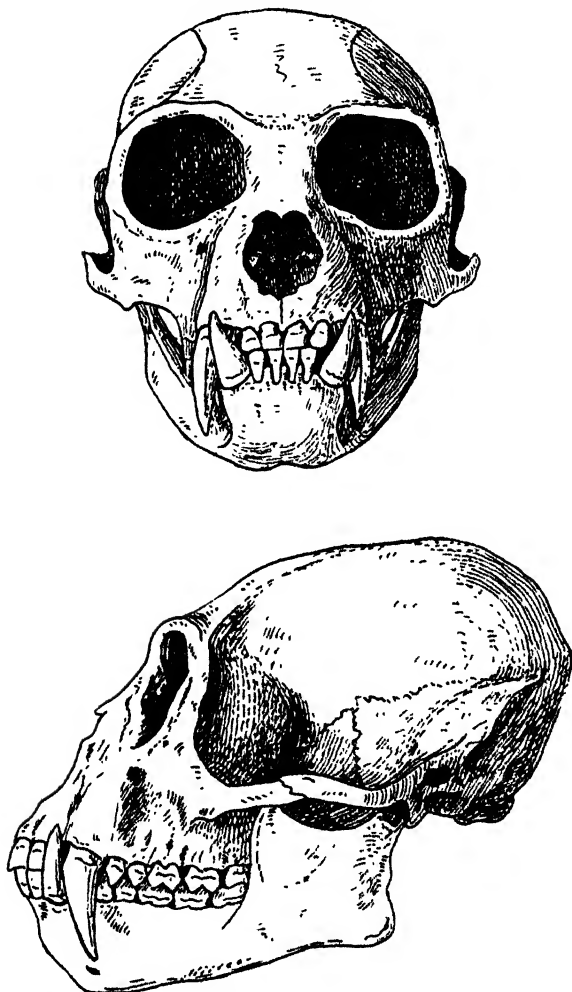
The colour of the young is variable. A young male from the North Shan States, weighing $2\frac{1}{2}$ lbs., is not so black above as the adults in the dark phase, and is decidedly brownish on the cheeks and chest; there are some greyish-brown hairs round the genitalia, but the preputial hairs are black. A half-grown male from Sadya, Assam, is brown, with the rump, thighs, and ventral surface dirty buff.

In the adults of both sexes the callosities and the nearly naked skin round the anus and the genital area are less exposed and to a greater extent concealed by the surrounding hairs than in *H. lar*; and in the adult males the preputial tuft, which may possibly vary seasonally, is much larger than in that species.

Sometimes it is remarkably large, consisting of long, wavy, harsh hairs, simulating a beard.

The approximate measurements of the head and body, in

Text-figure 20.

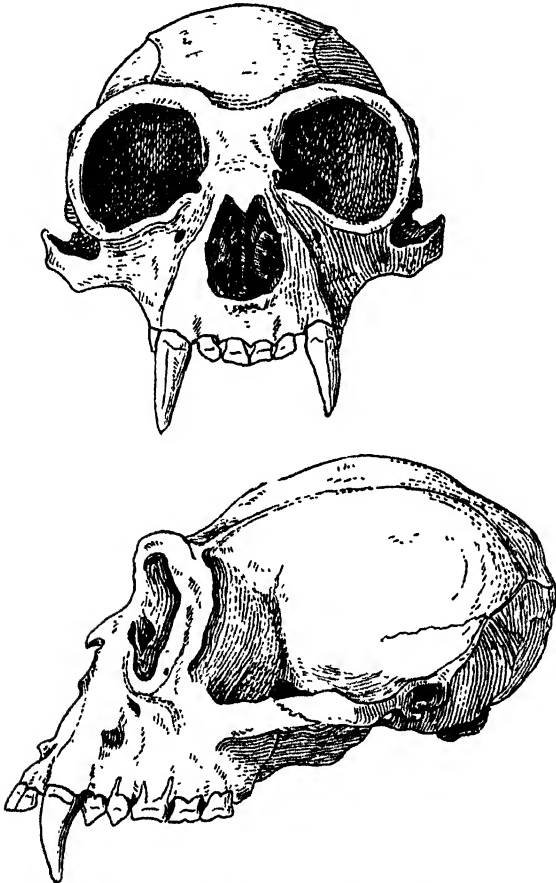


Skull of *Hylobates hoolock*, ad. ♂, from H'Kanti, Upper Chindwin
 $\frac{2}{3}$ nat. size.

inches, and of the skull, in millimetres, show that *H. hoolock* is somewhat larger than *H. lar*; and the skull further differs from that of *H. lar* in having larger teeth, more massive upper

jaws, relatively narrower orbits and, typically at all events, less well-developed brow-ridges. (Text-figs. 20, 21, pp. 731, 732.) The skulls vary individually to a considerable extent in the height and length of the cranial portion, the development of the brow-ridges, the slope of the nasals, the size and shape of

Text-figure 21.



Skull of *Hylobates hoolock*, ad. ♂, from Homalin, Upper Chindwin.
¾ nat. size.

the orbits and of the anterior nares, and other particulars; and some of them are not always easy to distinguish at a glance from some skulls of *H. lar*. Some of these variations may be seen in the sketches of the skull of two full-grown males from Upper Chindwin, the example from Homalin with the thickened orbits being an older animal than the other from H'Kamti.

Distribution. Assam (Lakhimpur, the Naga and Garo Hills, Cachar); Upper Burma (Kachin Hills, Upper Chindwin, Bhamo, the Northern Shan States, Manipur); Chittagong: and, it is alleged, even Arakan and Martaban in Lower Burma.

The range of this species to the north, east and south of Assam and Upper Burma is uncertain. The specimens I have seen came from Lakhimpur, the Naga Hills and other parts of Assam, and from the Upper Chindwin and the North Shan States in Upper Burma. The discovery of this Gibbon by the Mammal Survey of India at Lakhimpur adds colour to the claim by Pemberton, which was disputed by Blanford, that it is found in the hills of Bhutan.

It has been claimed by Tickell and Anderson that this species occurs in Lower Burma, Arakan, Pegu, etc., and that *H. lar* is found as far north as those districts in company with *H. hoolock*. I have seen no examples of either species from those districts. Blanford admitted the occurrence of *H. hoolock* in Arakan and Pegu, but disputed the extension of *H. lar* so far to the north. The possibility of confusion between the species must be borne in mind, because in the pale phase the two are not unlike. In *H. lar*, however, the dorsal surface is not so dark as in *H. hoolock*, and the ventral surface, although sometimes a little darker than the dorsal, is never so deep a tint as in the pale phase of *H. hoolock*, and the whiteness of the hands and feet and of the rim round the face is conspicuous at close quarters.

Judging from the material at his disposal, Blyth thought the two colour-phases of *H. hoolock* were sexual, the males being black and the females brown. This view was quite correctly disputed by Blanford, but was revived by Elliot in 1913. It is nevertheless approximately true. All the male specimens I have seen exhibited the black phase and all the females, except one, the pale phase. This exceptional female, which the collector erroneously sexed as a male, came from H'Kanti in Upper Chindwin. She is black, faintly tinged with brown, and has some greyish hairs on the sides of the face and a dirty white patch behind the chin.

The following are the approximate measurements, in English inches, and the weights, recorded by the collector of the Mammal Survey, of some examples of *H. hoolock* :—

Locality.	Sex.	Head and Body.	Hind Foot.	Weight.
Hati Khali, Cachar Hills . .	♂	25—	6+	17½ lbs.
H'Kanti, Upper Chindwin . .	♀	24½	6+	14½ „
Homalin, „ „ . . .	♂	24+	6+	16 „
H'Kanti, „ „ . . .	♂	24	6+	15 „
„ „ „ . . .	♂	23½	6	13½ „
Goktiak, N. Shan States . .	♂	23	6+	14½ „
„ „ „ . . .	♀	23	6—	„
Nargharita, Naga Hills	♀	20	5½	14 „

The following table shows some measurements, in millimetres, of skulls of *H. hoolock* :—

Locality.	Sex.	Total length.	Basal length.	Lg. of Palate.	Lg. of Upper Molars.	Orbital width.	Zygomatic width.
H'Kanti, Upper Chindwin ...	♂	115	85	40	28	65	74
Do. Do.	♀	113	84	41	30	67	76
Mokokchung, Naga Hills...	♂	113	86	44	28	64	76
Sadya, Assam	♂	111	85	44	30	65	71
Homalin, Chindwin	♂	109	80	40	30	66	76
Assam	♀	109	83	40	29	63	71

To the synonymy of *H. hoolock* I have added the name, *H. fuscus*, given by Winslow Lewis in 1834 to a couple of Gibbons purchased from the menagerie of a rajah in Calcutta, and stated to have come from the "vicinity of the Himalay Mountains." The author was interested in the Apes' anatomy, not in their specific characters, and merely described the colour as "dirty brown." By Anderson, and, following him, Forbes, *H. fuscus* was regarded as doubtfully identical with the Bornean Gibbon. They thus neglected the locality of the original specimens. Elliot treated *H. fuscus* as a separate form of doubtful status without venturing to suggest its affinities with any of the others he described, adding, however, that "the vicinity of the Himalay Mountains might mean anywhere."

It must be conceded, however, that the Gibbons exhibited in the menagerie of an Indian rajah and sold in Calcutta are more likely to have been examples of the Hoolock than of any other kind of Gibbon; and the Hoolock is the only Gibbon which can truthfully be said to live in the vicinity of the Himalay Mountains. And since an author without interest in details of coloration might, in my opinion, very reasonably dismiss as "dirty brown" the tint of Hoolocks exhibiting the pale phase, I can find no grounds for objecting to my identification on the score of colour. Winslow Lewis, however, fortunately gave a figure of the skull of *H. fuscus*; and this agrees in the contour of the facial region more closely with the skull of *H. hoolock* than with the skull of any of the subspecies of *H. lar* or of *H. concolor*, here admitted.

Examination of the type of *H. choromandus* Ogilby, preserved in the British Museum, confirms the opinion of previous workers that this Gibbon is an example of *H. hoolock* in the pale phase. It is a young individual, tawny or buff above, brown below, and on the cheeks, with the face encircled with a pale band, which is broader and more conspicuous than usual.

Ogilby gave the name *scyritus* to the Hoolock of the Assamese without describing it.

HYLOBATES CONCOLOR Harlan.

Distinguishable from *H. lar* and *H. hoolock* by the mode of growth of the hair on the crown of the head, which, instead of lying flat, is more or less erect, and in adults forms a mat or even a crest, higher in the middle than at the sides*; by the pinna of the ear being fused to a greater extent with the skin of the head, its posterior margin being inserted at a point somewhat above the upper edge of the antitragus instead of some distance below it†; and by the presence in the female of a long clitoris, grooved below, which depends beneath the vulva, simulating the penis of the male‡. Also there is no white or pale brow-band in either the black or buff phase of colour.

The skull, judging from the scanty available material, differs from those of *H. lar* and *H. hoolock* in the slope of the inter-orbital septum being inclined and continuous with that of the forehead, in the smaller brow-ridges and the more lengthened jaws. The facial portion of the skull is lower and the jaws less massive than in *H. hoolock*; and the orbits are relatively narrower and have less thickened rims than in *H. lar*.

Distribution. Indo-China: Tonkin, Hainan, Annam, Laos, and Siam.

The name *concolor* has been assigned by recent systematists to two distinct species of *Hylobates*. Trusting to the correctness of Harlan's statement that the type came from Borneo, Anderson (Zool. Res. Yunnan, p. 11, 1878) and, following him, Forbes (Handb. Prim. ii. p. 155, 1894), and Elliot (Rev. Primates, iii. p. 171, 1913) adopted it for the Bornean Gibbon described by Martin as *H. mulleri*. Matschie (SB. Ges. Nat. F. Berlin, 1893, p. 211), on the other hand, judging apparently from the wholly black colour of the type, applied the name to the species Thomas subsequently described as *hainanus*. In this he was followed by Pousargue (Bull. Mus. Paris, 1900, p. 272). Although when discussing on previous occasions the species of Gibbon now under notice I left its correct name unsettled, I now accept Matschie's verdict: and my reasons for so doing are as follows:—

- (1) Like Pousargue, I am unable to find any evidence of the existence in Borneo of a wholly black Gibbon. As stated above, Bornean Gibbons, which I regard as a subspecies of *H. lar*, may be black below and brown above, but there is always at least a pale brow-band. The only entirely black Gibbons known are some examples of the present species

* This crest is well shown in the copy of a photograph of a black phase of the female specimen from Hainan reproduced on pl. v. illustrating my paper on the Hainan Gibbon (Proc. Zool. Soc. 1906, pp. 169-180).

† See my paper on "The External Characters of the Catarrhine Monkeys and Apes" (Proc. Zool. Soc. 1925, pt. 4, p. 1493, text-fig. 37. B).

‡ See my paper quoted in the last note, p. 1555, text-fig. 75, C.

- and the Siamang; and the Siamang is excluded from consideration, as I pointed out in 1905, by Harlan's statement that the type of *H. concolor* had no guttural sac.
- (2) Harlan described and figured the clitoris of the type of *H. concolor* as very long and penis-like. A precisely similar clitoris was observed by Pousargue in the type of *H. nasutus* which came from Tonkin; and the clitoris of the living adult female from Hainan I described was also so long that the donor of the animal to the Zoological Gardens regarded it as a male, just as Harlan regarded the type of *concolor* as an hermaphrodite. In Bornean Gibbons the clitoris is quite different and resembles that of *H. lar*.
 - (3) I formerly rejected the name *concolor* for the Hainan Gibbon because of Harlan's statement that the coat of his specimen was thick, woolly, and frizzled, whereas in the three specimens of the Hainan Gibbon which I had then seen it was smooth and depressed. But further experience with this group of Apes has shown that the coat varies individually in the particulars mentioned, sometimes to a remarkable extent, probably with season, altitude, and age. Hence its length and texture are not dependable as systematic characters.
 - (4) From the positive evidence supplied by the colour and by the structure of the clitoris the conclusion seems unavoidable that the specimens to which the name *concolor* was given came from Hainan or the adjoining mainland of Tonkin, and not from Borneo. Probably it was secured from a dealer or was the pet of some private owner: and those who have received animals from such sources know how completely unreliable is the information supplied regarding the country of their origin. A century ago this would be still more true than it is at the present time.

The scanty material of this species at present available may be assigned provisionally to three subspecies based upon the colour of the throat and cheeks in the black phase. They may be distinguished as follows:—

- a. Cheeks and throat black, matching the rest of the pelage *concolor*.
- a'. Cheeks and throat pale and sharply contrasted with the rest of the pelage.
- b. Cheeks and throat white *leucogenys*.
- b'. Cheeks and throat reddish-buff *gabrielle*.

I am unable to find any characters distinctive of these forms in the pale or buff stage; and it is necessary to remember that other races of Gibbons, e.g. *H. lar pileatus*, differ individually in the colour of the cheeks as much as the three races of *H. concolor*, here provisionally admitted.

Subspecies CONCOLOR Harlan.

Hylobates concolor Harlan, Journ. Acad. Nat. Sci. Philad. v. pt. 2, p. 231, pls. ix. & x. 1837.

Hylobates harlani Lesson, Bull. Sci. Nat. Paris, xiii. p. 111, 1827 (proposed as substitute for *concolor*).

Hylobates niger Ogilby, Proc. Zool. Soc. 1840, p. 20 (*errore* for *concolor* Harlan).

Hylobates nasutus Kunkel d'Herculais, Sci. et Nat. ii. pp. 86-89, fig., 1884; also referred to, although not described, by A. Milne-Edwards, Le Nat. 1884, p. 497.

Hylobates hainanus Thomas, Ann. Mag. Nat. Hist. (6) ix. p. 145, 1892; Pocock, Proc. Zool. Soc. 1905, p. 160, pl. v.; *id. op. cit.* 1925, pp. 1493 and 1555.

Hylobates henrici Ponsargues, Bull. Mus. Nat. Hist. Paris, 1896, p. 367.

Two colour-phases in the adult, the black phase showing no trace of a white or buff patch forming a half-collar round the throat and cheeks; the pale phase buff, ochraceous-buff or greyish-buff, with a black or dusky patch on the crown of the head and extending on to the nape of the neck.

Distribution. Tonkin and Hainan.

The type of *nasutus* came from the coast near Along Bay in Tonkin, of *hainanus* from Hainan, and of *henrici* from Laichan in Tonkin, near the Yunnan border.

The types of *concolor*, *nasutus*, and *hainanus* exhibited the black phase of pelage, of *henrici* the pale phase.

So far as I am aware, there is no evidence of the occurrence of the buff phase in males, and this phase may be the final colour of mature females. But, as I showed in 1905, an individual female may exhibit both these phases and others in the course of her life. This was established by observations upon an example from Hainan presented to the Zoological Society by Mr. E. H. de St. Croix. When first procured, in July 1897, at the presumed age of six or seven months, this Gibbon was a dark smoky-grey, as her owner informed me. She soon, however, turned black; and totally black she remained until January 1904, when she was about seven years old, had attained her full size, and was sexually mature, as indicated by the appearance of menstruation. It was in January 1904 that Mr. de St. Croix brought her to England and deposited her in the Zoological Gardens; and within a few months of her arrival she began to turn grey, apparently by a process of bleaching of the pelage. The bleaching, however, did not take place uniformly all over the body. When it had been in progress for about three months, there was a black patch on the head and nape, bordered on each side of the crown by a grey band reaching from the eyebrow to the ear, the throat was white, and the general hue of the body blackish-grey with a considerable quantity of blacker hair on the sides of the belly close to the thigh, a broad triangular black patch reaching from the collar-bones to the fore part of the belly and bordered by a grey area paler than the back, the upper portion of the arms and legs

being paler than the lower. The black, however, gradually faded away until it finally disappeared, except on the crown of the head. In May 1905 she was brown or silvery-grey all over, with black superciliary vibrissæ, a few black hairs on the fingers and toes, and a black cap on the head, broadest and blackest between the ears, fading into brown upon the forehead and narrowing towards the nape of the neck.

In the black phase this Gibbon was exactly like the types of *concolor*, *nasutus*, and *hainanus*, and in the pale phase like the type of *henrici*; and since the type of *henrici*, like the type of *nasutus*, came from Tonkin, I have added *henrici* to the synonymy of this race, in which the black phase has black cheeks, although Thomas, as explained below, regarded it as a synonym of *leucogenys*, in which the black phase has white cheeks.

No adult skulls of this race are available for description, and no measurements taken from freshly-killed specimens have been recorded.

Subspecies *LEUCOGENYS* Ogilby.

Hylobates leucogenys Ogilby, Proc. Zool. Soc. 1840, p. 20; Thomas, Proc. Zool. Soc. 1927, p. 42.

Black phase exhibiting a white patch on the throat and cheeks which does not involve the corners of the mouth or lower lip. Pale phase golden-buff, varying here and there in intensity throughout, except for a blackish patch on the crown of the head and the nape.

Distribution. Siam and Laos.

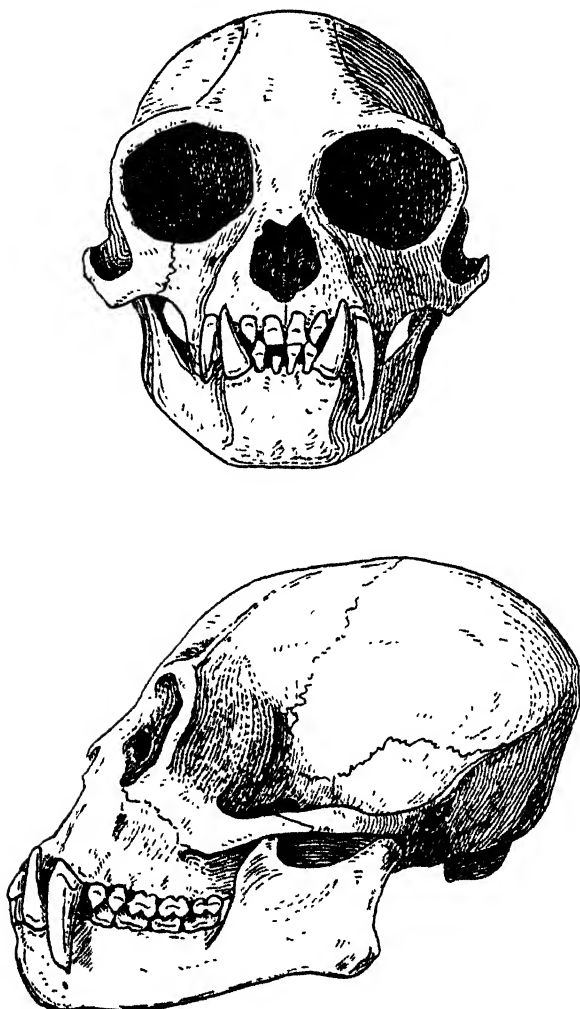
There are four examples of this race in the Natural History Museum—namely, Ogilby's type, a young male, ticketed Siam, an adult male and female from Xien Quang Koo, and a young one from Surannaket in Laos, collected by Messrs. Delacour and Lowe, as recorded by Thomas.

The adult male from Laos only differs in size from the type; but the female is golden-buff in general tint, with a black patch on the head and nape, as above described. Except in being a little brighter coloured, as would be expected in a wild specimen, she differs in no important point from the female of *concolor* from Hainan as I described her in 1905 after she had changed from black to greyish-brown or buff. She also does not differ, as Thomas pointed out, from the type of *henrici*; and on the strength of this resemblance he added *henrici* to the synonymy of *leucogenys*. It is needless to add that the similarity in the pale phase between the females from Hainan, Tonkin, and Laos is corroborative evidence of the close affinity between the Gibbons here grouped together as *H. concolor*.

Further evidence on this head is supplied by the changes of colour through which these Gibbons pass. According to Delacour, as quoted by Thomas, the young of both sexes of *leucogenys* is at first pale and then turns black; but whereas the

male remains black for the rest of his life, the female again turns pale. The very young specimen from Surannaket is tawny, but

Text-figure 22.



Skull of *Hylobates concolor leucogenys*, ad. ♂, from Xien Quang Koo, Laos.
½ nat. size.

the moulting which is in process shows that the tawny hair would have been replaced by blackish-grey pelage. This was the colour-phase exhibited by the young example from Hainan when

it first came into the hands of Mr. St. Croix, who presented it to the Zoological Gardens, and this Gibbon subsequently passed through exactly the same colour-change as that which M. Delacour now records as occurring in *leucogenys*.

The approximate dimensions, in inches, of the adults from Laos, as recorded by the collectors, are as follows:—

Sex.	Head and Body.	Hind Foot.	Ear.
♂	22	5½ +	1½
♀	21½ +	6—	1½

These measurements agree very closely with those of *Hylobates lar*, but indicate an animal smaller on the average than *H. hoolock*.

The measurements, in millimetres, of their skulls are as follows:—

Sex.	Total length.	Basal length.	Lg. of Palate.	Lg. of Upper Molars.	Orbital width.	Zygomatic width.
♂	113	80	43	27	67	78
♀	112	79	41	29	62	79

Subspecies GABRIELLE Thos.

Hylobates gabriellæ Thomas, Ann. Mag. Nat. Hist. (8) p. 112, 1909.

Differs from typical *leucogenys* in the colour of the patch on the throat and cheeks being rusty-buff instead of white, and in the extension of the patch to the corners of the mouth and a little way along the edge of the lower lip.

Distribution. Lang Bian, 1500 feet, 100 kilometres inland from Phanrang in Southern Annam.

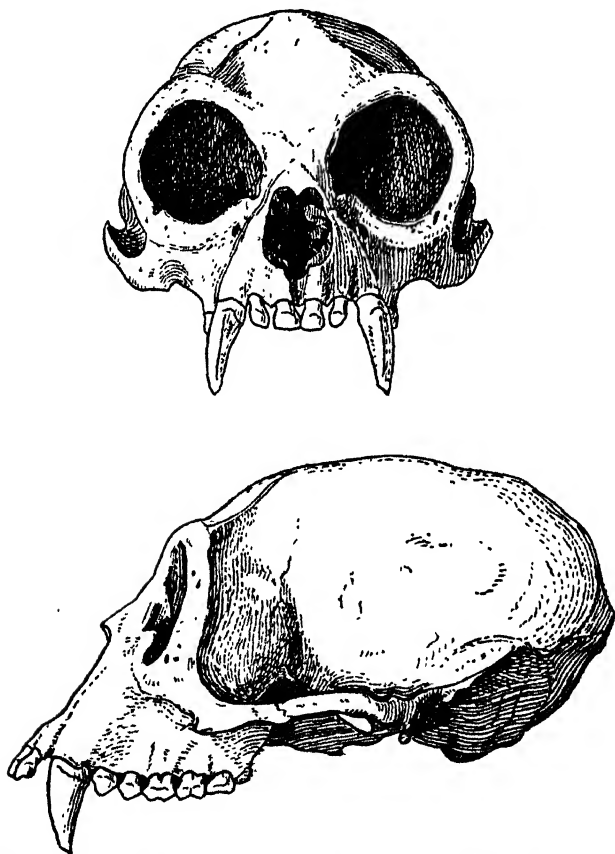
Only a single specimen of this race is available. It is an adult male exhibiting the black phase, the pale phase being unknown. Whether this specimen will ultimately prove to represent a race distinct from *H. l. leucogenys* must for the present be left unsettled. The differences are very slight and may prove to be of no systematic value.

The measurements, in millimetres, of the skull of this specimen are as follows:—

Sex.	Total length.	Basal length.	Lg. of Palate.	Lg. of Upper Molars.	Orbital width.	Zygomatic width.
♂	117	83	43	27	66	76

The skull differs in shape from that of the male of *H. leucogenys* recorded above, and has much more strongly developed orbital rims; but the differences between them, as shown by the

Text-figure 23.



Skull of *Hylobates concolor gabriellæ*, ad. ♂, from Lang Bian, Annam.
½ nat. size.

figures (text-figs. 22, 23, pp. 739, 741), are not greater than those between the two examples of the skulls of *H. hoolock* described and figured above (pp. 731, 732), and may be confidently ascribed to age and rejected as of no systematic value.



Fig. 1. R. G. S. & Danielsson, 1924

40. Some Barnacles in the British Museum (Nat. Hist.).

By C. A. NILSSON-CANTELL, Fil.Dr., Sweden *.

[Received April 1, 1927 : Read June 7, 1927.]

(Plate I.†; Text-figures 1-19.)

INTRODUCTION.

The descriptions published below are the fruits of work on the Cirripeds which I had the opportunity of carrying out during a sojourn at the British Museum, London, in the summer of 1925. For this opportunity I desire to acknowledge the kindness of Dr. W. T. Calman. By the loan of material it was possible for me to complete this work. My material contains, it is true, no species, new to science, but its value should not therefore be underrated, as I have in many cases taken up imperfectly-known species, for which more complete determinations are given. A number of Cirriped species have been very uncertain owing to imperfect descriptions. I was able to establish some as being synonymous, and to show that others which had been described from single individuals are merely variations of species already known.

The material is, in a certain sense, heterogeneous, being collected from various widely-separated localities and not the work of a single expedition or collector. The major part however, has been collected by English cable-ships belonging to the "Eastern and Associated Telegraph Companies."

Finally, it is of some interest to note that several new localities have been discovered, whereby our knowledge of the distribution of the Cirripedia has been increased.

DESCRIPTIONS.

Genus SCALPELLUM.

SCALPELLUM VELUTINUM Hoek, 1883. (Text-fig. 1.)

Scalpellum velutinum Hoek, 1883; Gruvel, 1902 *a*, 1905, 1920; Annandale, 1905, 1908 (?), 1911, 1916 (?); Pilsbry, 1907 *a*; Calman, 1918; Weltner, 1922; Barnard, 1925.

Scalpellum eximium Hoek, 1883.

Scalpellum sordidum Aurivillius, 1898.

Scalpellum erectum Aurivillius, 1898.

Scalpellum alatum Gruvel, 1902 *a*.

Discussion and complementary description.

This species described by Hoek displays some variations in the external parts which was the cause of several species being united

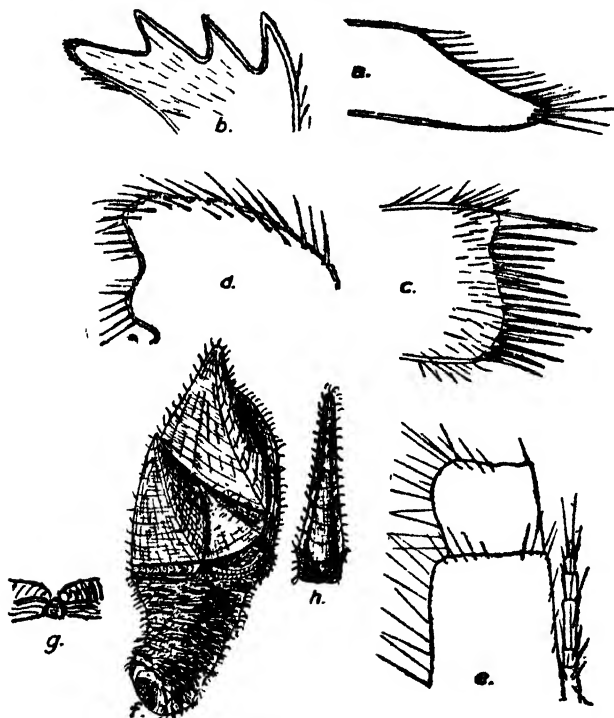
* Communicated by Dr. W. T. CALMAN, F.R.S., F.Z.S.

† For explanation of the Plate, see p. 790.

under this name by Gruvel (1902 *a* and 1920). Gruvel, at the same time, gave a lengthy description of the internal parts. Unfortunately, such descriptions are lacking for many allied species.

The figure of this species given by Annandale (1908, pl. iv. fig. 7) offers points of interest. The specimen represented seems externally to agree with other figures of the species, with the

Text-figure 1.



Scalpellum velutinum Hoek.

- a.* Palpus. *b.* Mandible. *c.* Maxilla I. *d.* Maxilla II. *e.* Cirrus VI. and caudal appendage. *f.* The animal, lateral view. *g.* Rostrum and rostral latera. *h.* Carina and carinal latera.

exception of the carinal latera, which are more projecting. This may, perhaps, be deemed an accidental variation, as Gruvel (1902 *a*) also represents similar examples. An allied species, *Sc. pedunculatum* Hoek, 1883, from New Zealand also has such carinal latera. In a later work (1916) Annandale figures the mandibles of his specimens of *Sc. velutinum* (pl. vi. fig. 6), which differ considerably from the description given by Gruvel (1902 *a*).

which description agrees with what I have found here. In the species of *Scalpellum* the mandibles appear to be fairly constant with regard to the number of teeth. Thus it is uncertain whether these specimens depicted by Annandale from the Indian Ocean (Gulf of Oman) really are typical *Sc. velutinum*.

In this connection it is worth mentioning that a specimen recorded by Annandale (1913) as *Sc. velutinum* got this name by some mistake. Calman (1918) has shown that it must be considered to be *Sc. annandalei* Calman, 1918.

A figure of my specimen is here given for comparison so as to avoid confusion when dealing with allied forms in the future.

The *mouth-parts* correspond closely to Gruvel's description.

Palp conical, with bristles along the edge and at the point.

Mandible with 3 teeth and a pectinated inner angle.

Maxilla I. with nearly straight edge without a notch.

Maxilla II. clearly bilobate, with a notch on the middle without spines.

Measurements (in millimetres): --

Length of capitulum, 30.

Breadth of capitulum, 19.

Length of peduncle, 18.

Breadth of peduncle, 12.

Number of segments of the Cirri * :--

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
11 16	22 24	23 24	24 25	28 28	27 28	7

Cirri I. and II. with rami of unequal length. The rest with rami of equal length. The longer cirri with 4 pairs of spines on the front edge.

Caudal appendages of about the same length as the first segment of the protopodite. The number of segments seems to vary somewhat, Gruvel giving 7-8, Calman 4-6. In any case the appendage is short and has few segments.

Locality. Singapore district. Eastern Extension, Australasia and China Telegraph Companies.

Distribution. The species is found in numerous localities of the Atlantic Ocean between Lat. 72° N. and Lat. 34° 32' S. (Gruvel, 1902 a; Barnard, 1925). Moreover, apart from Annandale's find, mentioned above, it occurs in the Indian Ocean and the Malay Archipelago. Usually obtained at depths from 35 to 1425 fathoms (64-2606 m.).

SCAPELLUM RUBRUM Hoek, 1883. (Text-fig. 2.)

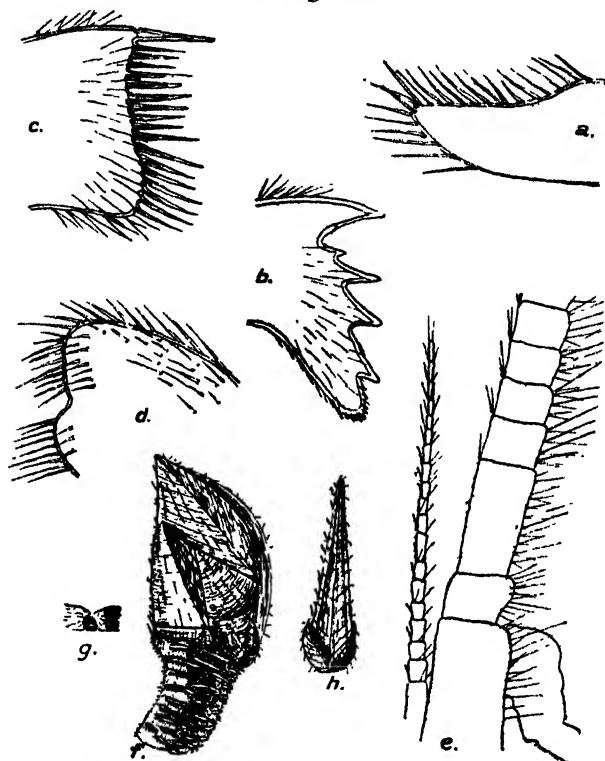
Scalpellum rubrum Hoek, 1883; Gruvel, 1905; Pilsbry, 1911; Calman, 1918; Broch, 1922.

* Number of segments are referred to the same individuals for which measurements are given.

Discussion and complementary description.

These four specimens from the Malay Archipelago resembled those described by Calman (1918) from the same region, as they were almost entirely, except the carina, without the red colour of the plates, which was supposed to distinguish the species. They

Text-figure 2.

*Scalpellum rubrum* Hoek.

- a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Cirrus VI. and caudal appendage. f. The animal, lateral view. g. Rostrum and rostral latera. h. Carina and carinal plate.

had, on the other hand, an evident green colour. This species is reminiscent of several others, wherefore Broch (1922) supposes that *Sc. rubrum* and *indicum* Hoek, 1883 may be regarded as younger individuals of *Sc. darwini* Hoek, 1883. However this may be, these specimens agree closely with the lengthy description by Pilsbry (1911), particularly in the inner parts and especially in the caudal appendages. An external similarity exists, for instance,

between *Sc. rubrum* and *Sc. uniarticulatum* Author, 1921. The latter is without bordering ribs on the carina, but this difference might conceivably be due to a difference of age. Examination of internal parts shows, however, that the species evidently differ in mouth-parts and caudal appendages. For comparison a figure of the animal is given with mouth-parts and caudal appendages (text-fig. 2).

As regards mouth-parts, one notes especially the mandible, which, according to Pilsbry, has 4 teeth and a multispinous inner angle. In the specimen I examined, one mandible had 4 teeth and the other a smaller 5th tooth between the original 1 and 2. In my opinion the number of teeth in the mandible has great systematic value. This species has never less than 4 teeth. Many species of *Scalpellum* have 3 teeth and an inner angle.

Maxilla I. also characteristic, with no notch on the front edge.

Maxilla II. with evident notch as in most *Scalpellum*-species.

Measurements (in millimetres):—

Length of capitulum, 23.

Breadth of capitulum, 14.

Length of peduncle, 18.

Breadth of peduncle, 11.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
8 12	18 22	— 24	24 26	24 25	26 26	19

This is in agreement with the statements of Pilsbry: cirrus I. with 8 and 11 segments, cirrus V. with 27 and 27, caudal appendage with 17; and Calman: cirrus V. with 25 and 25 segments, caudal appendage with 20.

New localities. Sahul Bank, S. of Timor, Lat. 10° 30' S., Long. 126° 35' E., 100 fathoms (183 m.), 1.9.1919. C. S. 'Recorder.' Pres. by Eastern and Associated Telegraph Companies.

Distribution. Japanese waters, Malay Archipelago.

SCALPELLUM MOLUCCANUM Hoek, 1883. (Text-fig. 3.)

Scalpellum moluccanum Hoek, 1883, 1907; Gruvel, 1905.

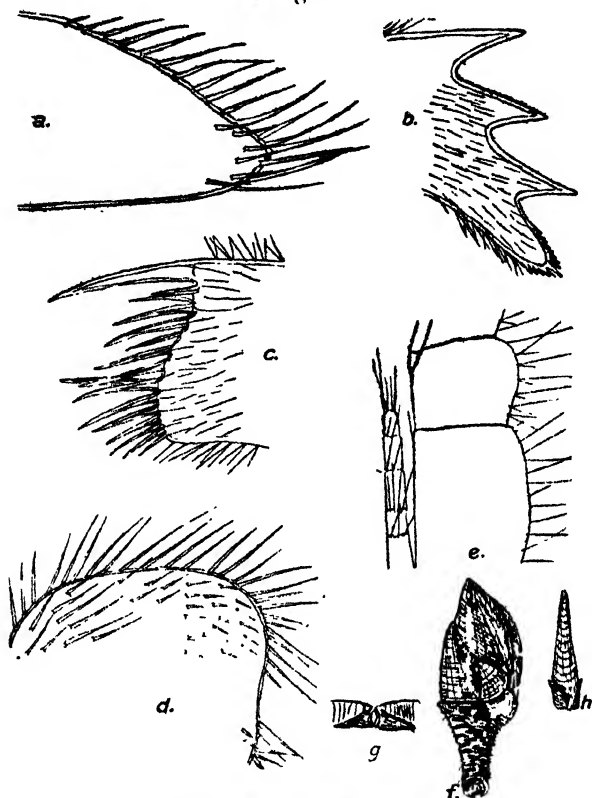
Discussion and complementary description.

Several externally rather similar species have been described—for instance, *Sc. moluccanum* Hoek, 1883, *Sc. regium* (Wyv. Thomson, 1877), *Sc. molle* Aurivillius, 1898; the first from the Malay Archipelago and the two latter from the Atlantic. As the inner parts of some of them have not been examined, it is hard to decide whether they are properly distinguished. The specimens from the Malay Archipelago and the Pacific here described are regarded as *Sc. moluccanum*, which I have been able to study closely in the collections of the British Museum. Hoek says of

the species 1883, p 106: "It is extremely difficult to decide whether one is right in considering the specimens taken at Station 195 as specifically distinct from *Scalpellum regium*."

The specimens of *Sc. regium* figured by Gruvel (1920, pl. i. fig. 7) agree fairly well with my own, the carina being provided

Text-figure 3.



Scalpellum moluccanum Hoek.

- a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Cirrus VI. and caudal appendage. f. The animal, lateral view. g. Rostrum and rostral latera. h. Carina and carinal latera.

with bordering ribs. This characteristic is not mentioned with regard to any species in Hoek's original description. *Sc. moluccanum* lacks a description of the inner parts which *Sc. regium* has, both by Hoek (1883) and Pilsbry (1907 a). My specimens

agree best with *Sc. moluccanum* as regards locality also. We are thus unable at present to decide whether the species are clearly distinguished. Hoek's statement as to the hairiness or hairlessness of the capitulum and as to the greater or less breadth of the carinal latus are certainly of no great value, since these characters are variable.

The appearance of the outer parts in my specimens will be plain from text-fig. 3. The external similarity to *Sc. rubrum* is very considerable. But this specimen is plainly divergent in the occludent margin of the capitulum, which becomes straighter and less convex than in *Sc. moluccanum*. This last character may possibly be subject to variation. This is, however, unimportant, as the species are plainly distinguished in other characters. A detail of some interest is whether the carina is dorsally convex or provided with bordering ribs. Pilsbry, like Hoek, finds in the typical *Sc. regium* a convex carina, but in the subspecies *latidorsum* it is concave with ribs. Gruvel's specimens (1920) also have bordering ribs on the carina, but are described as *Sc. regium*. Presumably there is here a certain variation. In my specimens there are very small and insignificant ribs. The value to be assigned to this character is thus doubtful.

Mouth-parts. Labrum armed with teeth.

Palp conical, of normal appearance.

Mandible with 3 teeth and a pectinated inner angle.

Maxilla I. with straight front edge, somewhat prominent underneath. Spines largest at the top.

Maxilla II. with a spineless slight notch on the middle of the front edge.

Measurements (in millimetres):—

Length of capitulum, 18.

Breadth of capitulum, 12.

Length of peduncle, 12.

Breadth of peduncle, 7.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
10 13	24 27	30 30	31 33	31 31	31 33	5

No penis.

The *caudal appendage* in the full-grown individual somewhat longer than the proximal segment of the protopodite. In the smaller, not full-grown individual, shorter, with only two segments. For *Sc. regium* 4–6 segments are given.

From the similarity of the inner parts of *Sc. regium* and *moluccanum* it may, perhaps, be concluded that the species are, at any rate, closely related.

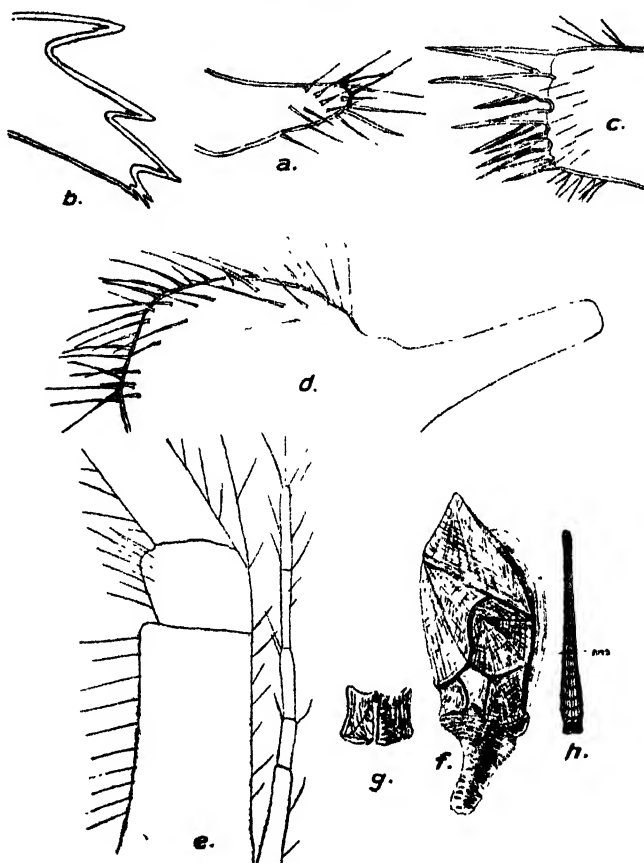
New localities. Lat. 37° S., Long. 163° 30' E., 1500 fath. (2745 m.), 6. 3. 1918. Pres. by Eastern and Associated Telegraph Companies.—Lat. 9° 16' S., Long. 117° 8' 35" E., 1380 fath. (2525 m.), 16. 7. 1907. Pres. by F. Wood Jones.

Distribution. Malay Archipelago. The Pacific between Australia and New Zealand. At great depths.

SCALPELLUM DISTINCTUM Hoek, 1883. (Text-fig. 4.)

Scalpellum distinctum Hoek, 1883, 1907; Gruvel, 1905.

Text-figure 4.



Scalpellum distinctum Hoek.

- a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Cirrus VI. and caudal appendage. f. The animal, lateral view. g. Rostrum and rostral latera. h. Carina and carinal latera.

Complementary description.

This species dealt with by Hoek (1883 and 1907) is here represented by a large specimen. As the species can easily be

identified and good descriptions exist, I shall only give a little supplementary information.

The agreement in the shape of the plates will appear from a comparison of text-fig. 4 and Hoek's figures of the species. As in Hoek's specimen, I find evident chitinous sutures between the plates and, moreover, the lines of growth of the plates are plainly visible. Hoek asserts (1907) that the streakiness of the plates is less evident than appears from pl. vi. fig. 10, 1883. There would seem to be some variation here.

The carina according to Hoek (1883) with the umbo at the apex; according to Hoek (1907) somewhat under the apex, which latter I also found in my specimens.

Another detail of interest is the rostrum, which, according to Hoek, is absent. The fact that occasionally an extremely reduced rostrum occurs is shown by this specimen (text-fig. 4), a fine instance of the constantly proceeding reduction of this plate.

The remaining plates agree with the statements of Hoek.

Peduncle, too, displays the same regular arrangement of scales in rows as in Hoek's individual—at any rate as regards the upper part of peduncle.

Measurements (in millimetres):—

- Length of capitulum, 19.
- Breadth of capitulum, 11.
- Length of peduncle, 6.
- Breadth of peduncle, 6.

Mouth-parts not previously depicted; described by Hoek (1907).

Palp conical, with spines at the point.

Mandible with 3 teeth and a short inner angle, delicately pectinated, as stated by Hoek (1907).

Maxilla I. with slight notch with strong spines at the top diminishing in size downwards.

Maxilla II. with long spines along the straight front edge which passes evenly into the upper edge, also provided with spines. Behind, a very well-developed maxillary lobe, which is also stated by Hoek.

Caudal appendage, which is here somewhat longer than the protopodite and composed of 5 joints, agrees well with the statement of Hoek.

Complemental male, described by Hoek, was not met with in this specimen.

New locality. Lat. $9^{\circ} 15' S.$, Long. $115^{\circ} 10' E.$, 800–1500 fath. (1440–2745 m.), 29. 3. 1916. Pres. by Eastern and Associated Telegraph Companies.

Distribution. The East Indian Archipelago, 711–1500 fath. (1301–2745 m.).

Genus *LEPAS*.*LEPAS ANATIFERA NONFURCATA*, var. n. (Text-fig. 5; Pl. I. fig. 1.)*Discussion.*

In determining Australian Lepadides at the British Museum, I came across some specimens which were in certain respects divergent from other known *Lepas* species. These are here described under *L. anatifera* as a new variety, *nonfurcata*, which may possibly be raised to the rank of a species when further finds have been made.

Several authors (e. g. Annandale, 1906, 09; Broch, 1924, etc.) point out the difficulty of distinguishing the species of *Lepas*. Annandale says (1906, p. 139): "It is often almost impossible to distinguish tropical examples of this species (*L. anatifera*) from *L. anserifera* by mere examination of the shell. The only safe method of distinguishing the two species is to examine the filamentous appendages." Many *Lepas* specimens have often been incorrectly determined just because the species have been deemed easily identifiable. The following will prove that this is not the case. Borradaile (1916) describes a new *Lepas* species, *L. affinis*, nearly related to *L. hillii*. Because the *Lepas* material of the 'Terra Nova' Expedition was divided between the British Museum and the Otago Museum, New Zealand, it also was described as *L. anatifera* var. c. by Jennings (1915). Borradaile (1917) points this out, and says: "My *Lepas affinis* is Mr. Jennings's *L. anatifera* var. c." Unaware of Jennings's work (1915) and Borradaile's (1917), I examined at the British Museum some specimens from Australia (Cambridge Beach)* which had been determined as *L. hillii*, and found them like Borradaile's *L. affinis*. I was, however, more inclined to class these, as well as Borradaile's *L. affinis*, as *L. anatifera* rather than as *L. hillii*. They can scarcely be regarded as a new species, since great variations are found in *L. anatifera*.

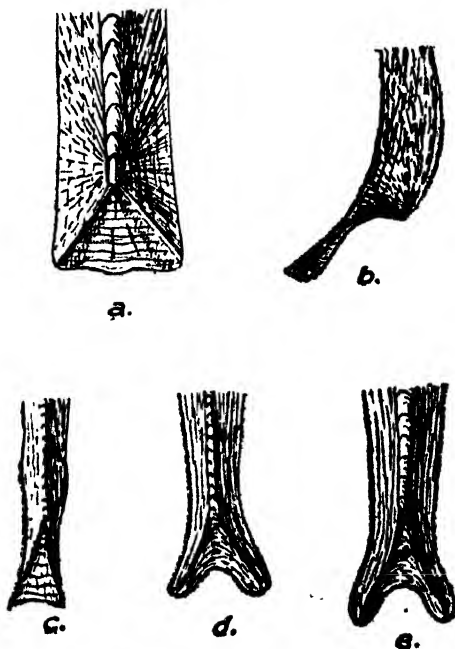
Of the *Lepas* species examined I have found *L. hillii*, *australis*, *pectinata*, and *testudinata* more easily determinable owing to the smaller variation. *L. anatifera* and *L. anserifera* seem to be more variable and difficult to determine. The outer parts vary very much, so that there are individuals which externally stand midway between these species. The lateral appendages are very helpful, as Annandale remarks. *L. anserifera* has several of these developed (4-6). In *L. anatifera* there are only two which are evident, the others being indicated by slight elevations. I have, moreover, satisfied myself of this by examination of the rest of the British Museum's material of this species.

* This find from Australia seems to indicate that the specimens taken by the "British Antarctic Expedition" from the bottom of the Expedition's ship, 'Terra Nova,' in Lyttleton Harbour, are possibly derived from these southern waters, although the matter has not been absolutely decided. They may have been brought by the vessel from other more distant waters.

Description.

The plates of capitulum in var. *nonfurcata* were, as a rule, markedly striated—more than is usual in the case of *L. anatifera* specimens. In certain of the *Lepas* individuals which I found agreeing with Borradaile's *L. affinis*, some striation of the scutum could also be observed, which indicates that these variations ought not to be regarded as specific. The occludent margin of capitulum is rather markedly convex, which is not usually the case with *L. anatifera*. The plates are not

Text-figure 5.

*Lepas anatifera nonfurcata*, nov. var.

a. Carina, dorsal view; b. Lateral view. c, d, e. *Lepas testudinata* Auriv., carina, dorsal view.

separated by wide chitinous sutures. Scutum and tergum of the usual appearance. No internal umbonal teeth were met with on either scutum. I have found this tooth more or less plainly developed in different specimens of *L. anatifera*.

Carina has an appearance characteristic of this subspecies, not being bifurcated underneath, which is otherwise the case in *L. anatifera*. This præumbonal part is a small disc of the width of the rest of the carina (text-fig. 5, a, b). A certain resemblance

may be traced in this to *L. testudinata* Auriv., 1894, but this species has the præumbonal part also forked. Text-fig. 5 shows a series drawn from the type-material of Aurivillius. Jennings (1915) mentions that *L. australis*, when young, can have a carina without prongs developed. It is certain that the forms described here are not young individuals, since both large and small lack any trace of a forked carina.

Peduncle I find in my specimens to be rather short and, as a rule, provided with small chitinous spines which in some specimens were absent.

Measurements (in millimetres):—

- Length of capitulum, 27, 30.
- Breadth of capitulum, 18, 19.
- Length of peduncle, 5, 12.
- Breadth of peduncle, 3, 5.

Mouth-parts and other inner parts I found agreeing with the other *Lepas anatifera*-individuals examined, so that no further description is needed.

Localities. Cottesloe, near Perth, Australia, 7. 8. 1922. On the shell of a cuttle-fish. C. L. Glauert.—Australia, 23. 9. 1863. On the shell of a cuttle-fish. Bowerbank.—Wellington, Otago Univ. Museum, 1886.

Genus HETERALEPAS.

Syn. Author, 1921.

Several systematists have rightly dwelt on the difficulty in determining species of this genus. Broch (1922, p. 280) writes: "We must await such a revision before we can hope to get a solution to many questions concerning this intricate genus." The following discussion cannot be regarded as the revision which is awaited, but if it can in some measure contribute to that end something will be gained. Such a revision would require the examination of all museum material and the collection of a further quantity. In determining a large material of the subgenus *Heteralepas*, I was constantly confronted with such difficulties. A contributory cause is the fact that many species were described prior to Pilsbry's revision and division of the genus into the subgenus *Heteralepas* and *Paralepas*. It was natural that attention was not until then directed to those significant characteristics which distinguish the two genera. That is why difficulties still exist when it has to be decided whether the descriptions are to be referred to the one or the other subgenus.

Thus, e. g., the two species *H. lithotryæ* Hoek, 1907 and *H. morula* Hoek, 1907 were placed by Krüger (1911) under the subgenus *Heteralepas*, but by Barnard (1924) under the subgenus *Paralepas*. I believe the latter author is right. The smaller differences of length of the rami in cirri V. and VI.,

according to Hoek, for these species are not essential, and are not comparable with the conditions in the subgenus *Heteralepas*. In both these species, moreover, the bristles are those typical for the subgenus *Paralepas*. Furthermore, many species seem to me uncertain—to give a few instances: *H. tenuis* and *ovalis* Hoek, 1907. Others are mentioned under *H. japonica*.

In working over the material dealt with below, I have been able to establish that characters used as specific distinctions in this genus have been very variable. Particular importance has been attached to the external appearance of the animals. This has not always been wise. As this genus has lost its plates, it only remains, as regards the outer parts, to pay attention to the shape, the thickness, and folds of the cuticle etc. In this connection I have found great variations in individuals from the same locality; this may be due to age or even to manner of preserving. The capitulum may be more or less evidently marked; peduncle longer or shorter etc.

As to the inner parts, great importance has been attached in the subgenus *Heteralepas* to the shorter rami on cirri V. and VI., and likewise to the length of the caudal appendages and the number of segments of the cirri. These characters have, no doubt, in many cases great significance (Author, 1921), but here, as will appear from the following determinations of several specimens from different habitats, they do not seem reliable enough to distinguish species by. A contributory cause is also the fact that the segment-limits in the proximal parts are just here often indistinct. Krüger (1911) seems to have observed great variation in the number of segments. He says (p. 31): Für die *Heteralepas*-Arten ist die Gliederzahl der atrophierten hinteren Äste der fünften und sechsten Cirren von systematischem Wert. Dieser wird nun aber etwas problematisch, wenn man die folgenden Zählungen betrachtet." Therefore we shall probably find useless the distinguishing characteristics which in Gruvel's key to the genus are applied to the smaller length of the posterior rami in cirri V. and VI. The passage runs: "Rames des 5° et 6° paires atrophiées et égales" for the species *japonica*, *belli*, and others; "Rames des 5° et 6° paires atrophiées et inégales" for the species *lankesteri*, *indica*, etc. (see also the account of the number of the segments in *H. japonica*, p. 758).

Presumably we shall have to reduce the number of species in the future very considerably. A small beginning is attempted below, founded on a fairly abundant material and on studies of type-specimens in the British Museum, London.

HETERALEPAS (HETERALEPAS) JAPONICA (C. W. Aurivillius, 1894). (Text-fig. 6; Pl. f. figs. 2-4.)

Alepa japonica C. W. Aurivillius, 1894; Gruvel, 1905.

Heteralepas japonica Pilsbry, 1911; Krüger, 1911.

Alepa indica Gruvel, 1901, 1902 c, 1905.

Heteralepas indica Krüger, 1911.

Discussion.

The material from the Pacific Ocean and the Malay Archipelago dealt with below proved that the species *H. japonica* and *indica*, mainly distinguished by their internal characters, were very hard to separate. As the external characters, *e. g.* difference in the length of peduncle, also are liable to great variation, my opinion after this investigation is that, strictly speaking, the two species cannot be distinguished. Detailed reasons for this are given in the extended description below. *H. indica* is therefore only included here as a forma *indica* of *japonica*, and then concerns individuals with long peduncle. Possibly this variation need not be specially treated of in a future revision.

Other species related to *H. japonica* which may be subjected to examination by this revision are the following:—*H. nicobarica* Annandale, 1909, which, owing to its external similarity to *H. indica*, was first described by that author (1905) under the latter name; as the essential divergence is deemed to lie in inner dissimilarities which are disputable, it is uncertain. *H. gigas* Annandale, 1905, and *H. cygnus* Pilsbry, 1907 *a*, may become disputable for similar reasons; Pilsbry (1907 *a*, p. 102) says: "*Heteralepas gigas* is a larger species than *H. cygnus*, with the peduncle similarly lengthened." In this material I met with individuals of various ages which, judging by their externals, might well be deemed to belong to the above-mentioned species. In connection with *gigas*, to be sure, the occurrence of chitinous rudiments of the scuta, indicating descent from forms provided with plates, is also mentioned.

Complementary description.

A dorsal keel, sometimes provided with small elevations, particularly evident in *H. cornuta*, is found in most individuals of the genus; in certain cases, however, weakly developed (No. 2). It then extended the whole length of the animal. The limited dorsal tract of the capitulum mentioned in *H. lankesteri* I found in some specimens, as, for example, No. 4; in others it was lacking, as in Nos. 3 and 6. In some specimens I found here and there on the capitulum tracts marked in this way (No. 5). This character is thus of little systematic value. The cuticle, which was often strongly inspissated, was provided with small chitinous tubercles and hairs. In no case did I find such spines as are ascribed to *H. lankesteri*. The colour of the cuticle was in most specimens yellow to yellow-brown. In a few the cuticle had an evident green colour (Nos. 5 and 6). This, however, is of slight significance, as they were preserved specimens.

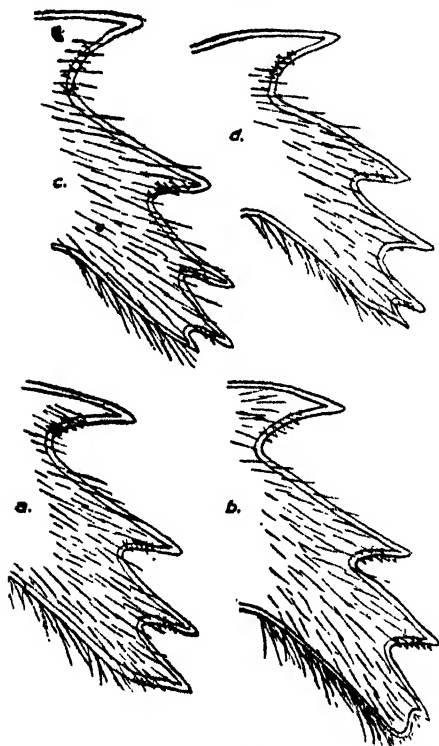
The variation in the length of the peduncle will appear from the table. Contractions under preservation must be taken into account. The difference of length may also be capable of a biological explanation (*cf.* short and long specimens of *B. balanoides*).

Mouth-parts. *Labrum* concave in all the specimens examined, with prominent teeth.

Palpus conical, with the appearance typical of the genus.

Mandible, according to the original descriptions, alike in *H. japonica* and *indica*, with three teeth and one tooth-like inner angle. In my material I find now 3, now 4 teeth and a clear inner angle. Between these two types one can find transition-types, when an extra tooth develops below which afterwards

Text-figure 6.



Heteralepas japonica Auriv.

Mandible:—a. No. 8. b. No. 4. c. No. 7. d. No. 6.

conceivably becomes a new inner angle. Consequently the number of teeth is somewhat variable in this species.

Maxilla I. with strong spines above; below an evident notch, sometimes with smaller spines. This notch may sometimes be lacking in certain specimens, as I found in No. 9. The lower part of the front edge very prominent, with clear spines. This

appendage in all the specimens examined is, broadly speaking, alike.

Maxilla II. protracted laterally, with a posterior bristly lobe. The spines of the front edge often divided into two groups, which, however, are sometimes continuous. Krüger (1911) says of *H. japonica*: "Die Mundteile zeigen überhaupt grösste Übereinstimmung mit denen von *H. indica*," which is probably correct.

Measurements (in millimetres):—

No.	Length of capitulum.	Breadth of capitulum.	Length of peduncle.	Breadth of peduncle.
1	9	6	5	5
2	30	23	33	13
3 <i>a</i>	21	20	59	9
3 <i>b</i>	10	8	18	4
4 <i>a</i>	10	14	48	8
4 <i>b</i>	29	22	82	14
5 <i>a</i>	21	13	54	7
5 <i>b</i>	13	10	8	4
5 <i>c</i>	36	22	116	15
5 <i>d</i>	20	15	33	6
6 <i>a</i>	17	13	12	8
6 <i>b</i>	33	23	45	19
7 <i>a</i>	13	10	19	7
7 <i>b</i>	13	11	30	8
8 <i>a</i>	21	20	55	9
8 <i>b</i>	21	16	14	9
9	21	15	15	8

Number of the segments of the Cirri.

It has been already pointed out that no great importance can be attached to the difference in the number of segments in *Heteralepas*, as it is very variable. In illustration of this circumstance I have counted the number of segments in several individuals from different localities. For comparison I may refer to the investigation of Krüger (1911).

No.	I.		II.		III.		IV.		V.		VI.		Caudal appendage.
1	9	14	26	34	31	39	34	—	13	36	13	37	4
2	18	24	59	60	61	62	61	64	24	69	20	68	12
3 <i>a</i>	12	20	40	48	53	57	60	62	29	65	27	64	9
4 <i>a</i>	15	25	43	—	55	55	54	61	24	60	25	59	9
5 <i>a</i>	12	26	45	61	56	59	61	61	24	64	25	64	10
6 <i>a</i>	12	24	41	45	44	49	50	54	27	53	24	53	9
7 <i>a</i>	15	29	46	53	—	62	—	62	22	63	20	62	8
8 <i>a</i>	12	26	42	55	54	60	57	61	24	64	22	64	9
9	12	21	38	43	46	54	53	54	18	54	16	64	10

From the foregoing table it will appear that the statement of the length of the posterior rami in cirri V. and VI. (unequal number of segments in *H. indica*, equal in *H. japonica*), which has been deemed significant, is without significance for the

distinguishing of the species, and cannot now be appropriately included in the key for their determination.

The length of the caudal appendage in relation to the protopodite is variable. In No. 1 it is very short, as the specimen examined is not yet full-grown. In others, *e. g.* Nos. 5 and 7, they reach somewhat above the proximal segment on the protopodite. Gruvel assigns 12 segments to *H. indica*, Aurivillius 9 to *H. japonica*, Pilsbry (1907 *a*) 7 segments. These specimens show a variation of between 4 and 12 segments.

No.	External resemblance with:	Locality.	Depth in fathoms.	Date.	Collector.
1....	<i>japonica</i> .	Lat. 7° 35' S., Long. 114° 30' 30" E.	73-175 (143-327 m.).	28. 7. 1917.	Eastern and Associated Telegraph Cos.
2	<i>japonica</i> .	Lat. 6° 58' S., Long. 39° 18' E.	270 (494 m.).	25. 9. 1911.	—
3 ..	<i>f. indica</i> .	Lat. 10° 22' 30" E., Long 120° 7' 30" E.	130-500 (238-915 m.).	8. 12. 1908.	Netley Hospital collection.
4. .	<i>f. indica</i> .	Lat. 10° 26' S., Long. 123° 15' E.	160 (293 m.).	29. 3. 1916.	Eastern and Associated Telegraph Cos.
5	<i>f. indica</i> .	Lat. 6° 15' N., Long. 93° 35' E., S.E. of Gt. Nicobar.	1040-1120 (1903-2090 m.).	30. 4. 1925.	Eastern Extension Telegraph Cos.
6	<i>f. indica</i> .	Lat. 10° 30' S., Long. 126° 35' E., Sahul Bank, S. of Timor.	100 (183 m.).	1. 9. 1919.	Eastern and Associated Telegraph Cos.
7 ..	<i>f. indica</i> .	Off Cochin China.	250 (458 m.).	26. 3. 1919.	—
8 ...	<i>f. indica</i> .	Singapore district.	—	—	Eastern Extension Australian and China Telegraph Cos.
9 ...	<i>f. indica</i> .	Seven miles east of North Cape, New Zealand.	70 (128 m.).	9. 2. 1917.	—

Distribution. Japanese-Malayan waters, Indian Ocean (eastern and western parts).

HETERALEPAS (HETERALEPAS) LANKESTERI Gruvel, 1900. (Text-fig. 7; Pl. I. fig. 5.)

Alepas lankesteri Gruvel, 1900, 1905.

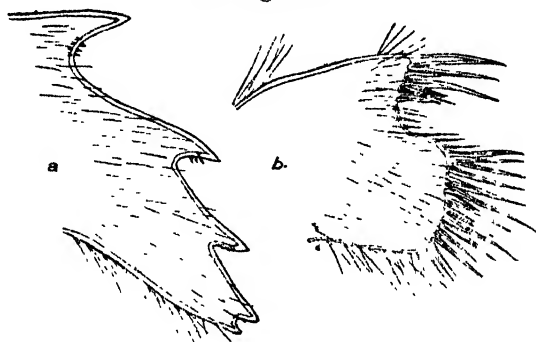
Complementary description.

This species, described by Gruvel (1900) from the West Indies, has been found here in 10 specimens. The species seems to me

to be closely related to *H. japonica*, as I was able to prove by a comparison of the material in the British Museum. As these specimens closely agree with Gruvel's description, especially in externals and locality, they are here included under this name.

Capitulum in all the specimens greatly swollen and the cuticle strongly thickened and transparent. On the surface the numerous irregular folds mentioned by Gruvel are noticeable even in uncontracted specimens, and are particularly evident around the tubular orifice. In the dorsal tract the cuticle in most specimens is less wrinkled, wherefore this part is often conspicuous, being separated by a crease from the ventral part. This latter circumstance, however, is not a characteristic of the species, the

Text-figure 7.



Heteralepas lankesteri Gruvel.
a. Mandible. b. Maxilla I.

same being found in other species I have examined. Something like this is mentioned in some species, e. g. *H. belli* and *microstoma* Gruvel, 1901. The capitulum, according to Gruvel, has no dorsal crest, but a slight continuous ridge. These specimens vary in this respect too, the ridge being more or less evident.

The *peduncle*, according to Gruvel, passes into the capitulum without a break. I find this to be so in smaller specimens. But in the larger specimens the boundary between capitulum and peduncle is more sharply defined. Peduncle, as a rule, is longer than capitulum. The chitinous processes mentioned by Gruvel, I also find in these individuals. Such do not appear to be the distinguishing features of this species solely.

Mouth-parts. *Labrum* with evident teeth.

Palp conical, with spines along one edge.

Mandible originally with 4 teeth and one lower more or less tooth-like angle. This angle is often missing. The lower edge of the teeth is often provided with small teeth.

Maxilla I. with very evident notch with small spines as in Gruvel's individuals, the lower part of the front edge projecting.

Maxilla II. with the appearance typical for the genus. Here, however, the spines of the front edge are not divided into two groups, but are continuous along the whole edge.

Measurements (in millimetres):—

Length of capitulum, 17, 25, 22.

Breadth of capitulum, 15, 22, 20.

Length of peduncle, 13, 34, 38.

Breadth of peduncle, 9, 13, 13.

Number of segments of the Cirri:—

	I.		II.		III.		IV.		V.		VI.		Caudal appendage.
	14	29	52	59	62	67	71	74	19	74	19	41	10
	16	26	65	77	—	73	84	84	21	92	22	89	12
After Gruvel.	13	21	50	55	—	—	—	—	19	—	16	—	10

The difference of length in the posterior rami mentioned by Gruvel seems from the above not to hold good, as my specimens have posterior rami on cirri V. and VI. of approximately equal length. The divergent number of segments in the longer ramus of cirrus VI. in the first specimen is because this ramus has been injured.

The *caudal appendage* in one of the specimens examined was longer than the protopodite, in another somewhat less. In this, too, there was a certain variation. For the rest I refer to Gruvel's descriptions.

Old locality. The West Indies, Mona Channel, 914 fath. (500 m.).

New locality. Lat. 7° 37' S., Long. 34° 26' 5" W., 50–150 fath (92–275 m.), St. Vincent-Peruambuco cable, 1.6.1917. Pres. by Eastern and Associated Telegraph Companies.

Genus PÆCILASMA.

PÆCILASMA KAEMPFERI Darwin, 1851. (Text-fig. 8.)

Syn. Author, 1921.

Discussion.

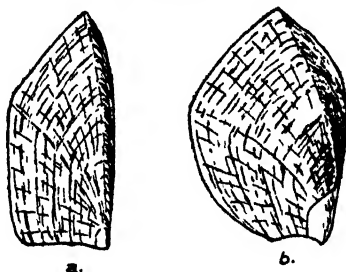
This species, which in minor details is rather variable, is represented by individuals from Japan and Tasmania, both of which appear to belong to Annandale's Race I. (typical form). The specimens from Japan were taken by the 'Challenger' Expedition, but, for some reason, were not described in Hoek's work (1883). This race, which, according to Annandale, is found in Japanese waters and the S. Pacific, is taken from those regions in this case also. The two subspecies *dubium* and *litum*, as also the species *P. inaequilaterale*, have been previously discussed (Author, 1921). Here I can only urge again that *P. kaempferi litum* still appears uncertain.

In his key Pilsbry (1907 a) says, for *P. kaempferi* (typical

form): "A narrow area between the ridge from umbo to apical angle of scutum and the occludent border"; for *P. kaempferi litum*: "A rather wide area between the ridge and the occludent margin." This feature I find particularly variable in these specimens, in some individuals the distance being great, in others indistinguishable (text-fig. 8).

The specimens from Tasmania seemed, as regards external parts, to agree with several of the classified subspecies. In Pilsbry's subspecies *novae-angliae* there is a strong ridge from the umbo to the tergo-carinal angle, and this was deemed to be lacking in *P. kaempferi* and *aurantia*. I found the same in these specimens from Tasmania; but as there was a similar feature in the above-mentioned specimens from Japan, no great significance can be

Text-figure 8.



Pacilasma kaempferi Darwin.

a, b. Left scuta.

ascribed to this character. In all likelihood these are also typical *Pacilasma kaempferi* individuals. Internally the specimens from both localities agreed.

Locality. Lat. 35° 11' N., Long. 139° 28' E., 'Challenger' Station 232.

New locality. Tasmania, Hobart. On *Pseudocarcinus gigas*, 15.10.1904. Pres. by Capt. Francis Mayors.

Distribution. (Race I), Japan, S. Pacific.

Genus OCTOLASMIS.

OCTOLASMIS NIERSTRASZI (Hoek, 1907).

Dichelaspis nierstraszi Hoek, 1907.

Octolasmis nierstraszi Author, 1921.

The seven specimens here examined resembled both in their external and internal parts those described by Hoek (1907). They varied in size from 5-9 mm. in length. The carina was in these individuals also evidently divided into two plates, a fact not mentioned by Hoek, but apparent from the figures (see further the Author, 1925).

Old locality. Malay Archipelago (different places).

New locality. Near Muskat, Persian Gulf, 21.7.1914. Pres. by Major S. G. Knox.

OCTOLASMIS HOEKI (Stebbing, 1894). (Text-fig. 9.)

Dichelaspis hoeki Stebbing, 1894; Gruvel, 1905.

Dichelaspis antiquæ Stebbing, 1894.

Dichelaspis aurivillii Gruvel, 1900, 1902 b.

Diagnosis. Capitulum compressed, with 5 plates. Scutum divided into an occludent segment and a broader basal segment, with lateral margin convex, straight, or hollow. The tergum when young approximately triangular, later on irregularly pentagonal. Carina with umbo near the base, ending below in a triangular disc. Length of peduncle varying up to greater than that of capitulum. The caudal appendage, one-jointed, of about half the length of the protopodite.

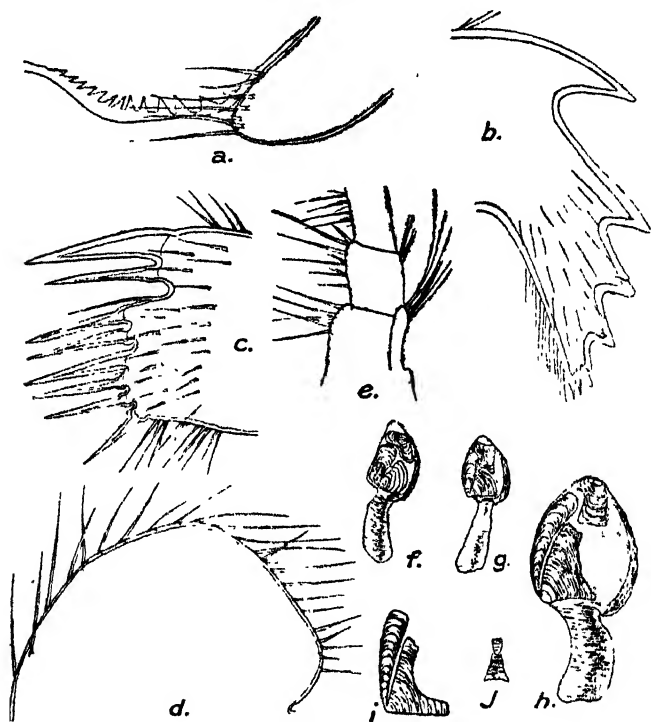
Discussion and complementary description.

The genus *Octolasmis*, which has embraced numerous species with very small differentiation, has recently undergone closer examination, whereby it has been shown that several species are very uncertain and that we probably have to do with small individual variations. Several associations of species have rightly been undertaken by Annandale (1909) and Barnard (1924). The present material affords great interest, as it comprises individuals of different ages. The latter also shows great variations with regard to the size and form of the plates. On the strength of this material I propose to gather the following into one species: *O. hoeki* (Stebbing, 1894), the allied (according to Stebbing) *O. antiquæ* from the same locality (Antigua, Antilles), and *O. aurivillii* Gruvel, 1900 from an unknown locality. Great importance has been attached to small differences in the shape of the plates, as was natural when the material was limited. At any final revision a further collection of species should certainly be made. More detailed reasons for this amalgamation will not be out of place.

The scutum is evidently divided into two segments as in the allied species *O. warwicki* (J. E. Gray, 1825). Of these the occludent segment is long and narrow and somewhat bent like the margo occludens of capitulum. Length of segment varying according to the age of the individuals (text-fig. 9). The basal segment in older individuals shorter than the occludent segment. In small specimens the segments may have the same length. In Gruvel's *O. aurivillii* the basal segment is fairly long. No great importance can be attached to this owing to the variation. The shape of the segment also is rather variable, which is an important factor in the case of an association of species. In young specimens (text-fig. 9, f, g), and occasionally in older ones, the margo carinalis on the segment is convex, but can in some be more or less straight

(text-fig. 9, *h*), as in the two species of Stebbing, and in extreme cases strongly concave (text-fig. 9, *i*), whereupon similarity arises with Gruvel's figure of *O. aurivillii*. The specimen figured in text-fig. 9, *f* with strongly convex margo carinalis had evident primordial valves. Such are found, although smaller, on Stebbing's figure of *O. antiquæ*, which, indeed, agrees fairly well with the one figured here. As the margo carinalis is somewhat

Text-figure 9.

*Octolasmis hoeki* Stebbing.

- a.* Labrum and palpus. *b.* Mandible. *c.* Maxilla I. *d.* Maxilla II. *e.* Cirrus VI and caudal appendage. *f, g, h.* The animal, lateral view, different stages. *i.* Scutum. *j.* Basal plate of carina.

straighter and the primordial valves smaller, Stebbing's individual is probably merely a somewhat older specimen than the one figured here (text-fig. 9, *f*).

An examination of the *tergum* shows likewise that the shape of this plate varies according to the age. In young specimens the corners of the *tergum* are rounded, whereby the plate obtains a practically triangular shape. Margo scutalis somewhat concave.

The primordial valve is situated on the middle of the plate. This shape corresponds pretty closely to the tergum figured for *O. antiquæ*. This species appears to me with certainty to be merely a later stage than the above-mentioned (text-fig. 9, *f*). This view is supported by the removal of the primordial valve nearer to the dorsal angle. Gradually, as the tergum is developed, the form characteristic of the species is obtained, this being represented in text-fig. 9, *g* and *h*, wherein *g* agrees most nearly with Gruvel's figure of *O. aurivillii* and *h* with Stebbing's figure of *O. hoeki*. The essential difference in the terga supposed to exist between Stebbing's two species, viz. "widening downwards" in *O. hoeki* and "narrowing downwards" in *O. antiquæ*, is, as shown by the foregoing investigations, merely a variation connected with age. In full-grown specimens the shape of the plate can hardly be referred to any definite geometrical figure; according to Stebbing it most closely corresponds to a trapezium, according to Gruvel to an irregular pentagon, which latter description seems nearest to the truth.

The *carina* in this species consists of a single plate. In some species, as, for instance, *O. warmicki* and *O. nierstraszi*, the plate consisted of two segments. The disc developed below is stated to have the front margin in *O. aurivillii* straight and dentated, in *O. hoeki* straight, and in *O. antiquæ* evidently though not deeply hollowed. Broadly speaking, it seems to me that the plate is alike in all. An examination of my material disclosed a certain number of small divergences in this character. The relative size of the plates in proportion to the capitulum is a question of some interest, as Stebbing states that the plates occupy a larger area in *O. antiquæ* than in *O. hoeki*. This agrees with my previous assumption that *O. antiquæ* is a younger individual of *O. hoeki*, for in my individuals the plates occupy a larger area of the capitulum in the younger than in the older specimens.

Peduncle is longest in *O. aurivillii*, shorter in *O. hoeki*, and very short in *O. antiquæ*. This dissimilarity is surely due to contraction under preserving.

Mouth-parts. *Labrum* concave, with strong teeth.

Palp conical, rounded, with few spines in my specimens.

Mandible in the specimen examined with 4 teeth and a lower finely-dentated angle. 3rd-4th tooth with additional teeth, which broadly seems to agree with the statements of Gruvel and Stebbing.

Maxilla I. with a notch in the upper part of the front edge, otherwise with strong spines on this edge. Comparing this with the statement of Gruvel and Stebbing, there appears to be some variation.

Maxilla II., not previously described, is provided with a straight front edge, passing away at the upper edge. Spines along the whole edge.

Measurements (in millimetres):—

Length of capitulum, 4, 3.
 Breadth of capitulum, 2.5, 2.
 Length of peduncle, 2, 3.
 Breadth of peduncle, 1, 1.

Number of segments in the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
<u>6</u> 7	9 9	9 9	9 9	9 9	9 10	1
6 <u>8</u>	9 9	9 10	9 9	9 10	— 10	1

The *cirri* are short, with a low number of segments. On the segments of the longer cirri are 4–5 pairs of spines on the front edge. A comparison of the descriptions shows the differences in the number of segments to be very small. This holds good, especially for cirrus I., which, according to Gruvel for *O. aurivillii*, has 6 and 7, according to Stebbing for *O. hoeki*, 6 and 7, and for *O. antiquæ*, 7–8. For the longer cirri, e. g. cirrus VI., Gruvel gives 10 and 10 segments. Stebbing accentuates a certain difference between his species, giving 8–10 segments for *O. hoeki*, 12–14 for *O. antiquæ*. This minor difference possesses surely no significance for distinguishing species.

The *caudal appendage* has one joint and is about half the length of the protopodite, with long spines at the point. This agrees well with the statement of authors. Stebbing gives a somewhat small difference between his species, which, however, seems to have little significance. It would have been more significant if the appendage had had differing numbers of segments. The foregoing discussion and description will suffice to show that the species represent different growth-stages of the same species: *O. hoeki*.

Old locality. Antigua, West Indies.

New locality. The Cape Verde Islands, São Nicolao. Pres. by Rev. R. B. Watson.

OCTOLASMIS LOWEI (Darwin, 1851). (Text-fig. 10.)

Dichelaspis lowei Darwin, 1851; Gruvel, 1905.

Dichelaspis darwini Filippi, 1861; Gruvel, 1902 b, 1905.

Dichelaspis aymonini Lesson, 1874.

Dichelaspis (Octolasmis) neptuni MacDonald, 1869; Gruvel, 1905; Barnard, 1924.

Dichelaspis (Octolasmis) sinuata Aurivillius, 1894; Gruvel, 1905; Annandale, 1909.

Dichelaspis (Octolasmis) trigona Aurivillius, 1894; Gruvel, 1905; Annandale, 1909; Weltner, 1922.

Dichelaspis mülleri Coker, 1902.

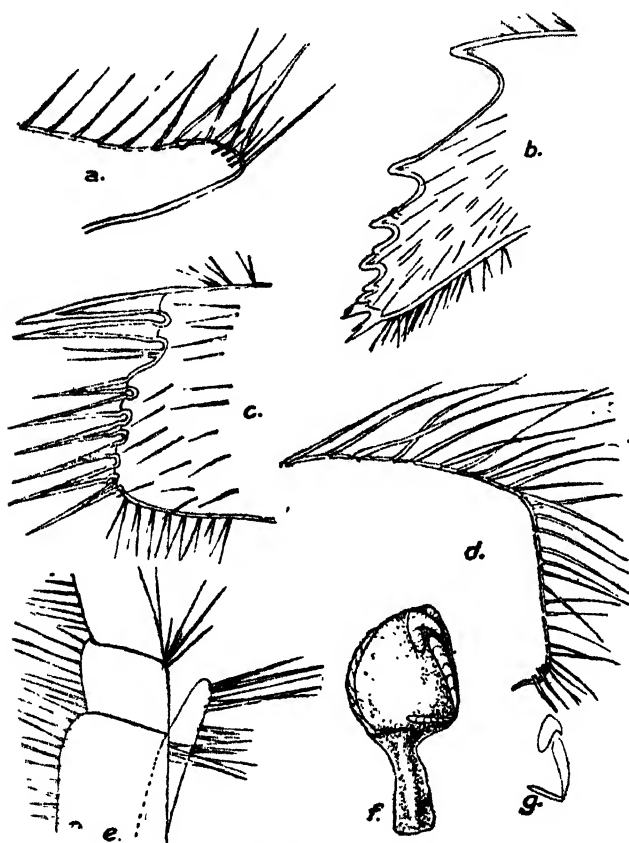
Dichelaspis vaillantii Gruvel, 1902 b, 1905; Annandale, 1909.

?*Octolasmis geryonophila* Pilsbry, 1907 a; Annandale, 1909.

Discussion and complementary description.

Annandale (1909) adopted as synonyms to *O. sinuata* Auriv., 1894 from Java Sea: *O. trigona* Auriv., 1894 and *O. vaillantii* Gruvel, 1902 *b* from Suez, which seem quite certain. As allied

Text-figure 10.

*Octolasmis lowei* Darwin.

a. 3rd Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Cirrus VI. and caudal appendage. f. The animal, lateral view. g. Scutum and tergum from left side of another individuum.

species Annandale adduces *O. neptuni* MacDonald, 1869 from Sidney; *O. mülleri* Coker, 1902 from Louisiana and North Carolina; *O. darwini* Filippi, 1861 from the Mediterranean; *O. aymonini* Lesson, 1874 from Japan; and *O. lowei* Darwin, 1851 from Madeira, and supposes that they may possibly be

united under *O. lowei* Darwin. This species would then be cosmopolitan. It is then tempting to assume that we have to do with local races. *O. geryonophila* Pilsbry, 1907 *a* from the Atlantic and, according to Annandale, also from the Indian Ocean seem to be kindred species, perhaps synonymous. Whether this, too, should be regarded as a local race cannot be decided as yet. The differences between the species, chiefly limited to the strongly reduced shape of the plates, or the animals seem insignificant. Both Annandale and the author (text-fig. 10) have found variations and intermediate specimens. The specimens described here from Tasmania ought most to resemble *O. neptuni* from Sidney, as, indeed, they do to a certain extent. However, I find specimens which agree very well with the figures of Aurivillius of *O. sinuata* and *trigona*. This lends further authority to the association of these two species. My material might then be described as *O. sinuata*, *O. trigona*, or even *O. neptuni*. Hoek (1883) says of *O. neptuni*: "I even think that it is more nearly related to *Dichelaspis lowei* Darwin than any of the other species." As, however, I have become more and more convinced that they can all be included under Darwin's species *O. lowei*, they are here described as such. Further finds will, no doubt, clear up this question of synonyms. As an instance of the great difficulties met with in the identification of the above-mentioned species, it can be stated further that Weltner (1922) regards some *Octolasmis* specimens from Japan as *O. trigona*, at the same time remarking that small divergences prevail with regard to the larger specimens. A comparison of Weltner's fig. 18, tab. iv. with the drawings of *O. aymonini* Lesson, 1874 (also from Japan) reveals a striking resemblance, especially as regards the shape of capitulum and tergum. This agrees with the pronouncement of Annandale (1909, p. 100): "Is *D. sinuata* distinct from the Japanese *D. aymonini* Lesson? So far as external characters go, I have examined intermediate specimens."

As an aid to future research into the forms concerned a complementary description and figures are given.

Capitulum compressed from the side.

Scutum consisting of two linear branches meeting one another at an angle. The basal segment in these individuals shorter and narrower than the occludent segment. The angle of the umbo less than 90°. The variation in the length of the branches appears from the accompanying figure. The differences prevailing between the different species in the development of the branches and the angle between them can probably be connected with the variation in the form of the capitulum, since the latter may have a more or less pointed apex, as appears on a comparison between, e. g., Darwin's fig. 8, pl. ii. 1851 and text-fig. 10 in this paper.

Tergum in typical specimens evidently saddle-shaped, herein agreeing best with Gruvel's fig. 14, pl. xiv. 1902 *b* of *O. darwini* and fig. 5, pl. xiv. of *O. sinuata*. In shape the plate can also be

unsymmetrical (text-fig. 10 *g*), resembling Darwin's figure of *O. lowei* and Aurivillius's fig. 8, tab. ii. 1894 of *O. trigona*, and several other species above-mentioned.

Carina in these specimens not reaching up to the tergum as in the species of Aurivillius. Cases, however, are mentioned where the carina is longer (Weltner, 1922, for *O. trigona*). In all the species described the lower part of the plate is evidently forked.

Mouth-parts. *Labrum* slightly concave, with dentated edge.

Palp conical, with spines at the point and along one edge.

Mandible with four evident teeth and a rudimentary fifth at the pointed lower angle. Additional teeth on 3-5. The distance between teeth 1 and 2 great.

Macilla I. with a slight incisure in the upper part. The spines of the front edge few, but strong.

Macilla II. with straight front edge. Spines evenly distributed along the front and upper edge.

Generally there seems to be good agreement with the descriptions of the mouth-parts given, especially as regards the statements of Darwin and Aurivillius.

Measurements (in millimetres):—







Length of capitulum, 4.

Breadth of capitulum, 3.

Length of peduncle, 2.

Breadth of peduncle, 1.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
						
5 7	12 13	12 12	12 12	12 12	12 12	1

The length of the first pair of the cirri was one-third of cirrus II. as Darwin states for *O. lowei*, with nearly equal rami. The number of segments of the longer cirri in the specimen examined was very constant. The segments in these bore 8 pairs of long spines in the front edge as in Darwin's specimens.

Caudal appendage as in Darwin's specimens with one joint, somewhat shorter than the protopodite of the sixth cirrus (the spines on the outer edge of the point not counted) (text-fig. 10, *e*). Aurivillius establishes for his species a small difference of length, surely of no significance for the distinguishing of species. In *O. vaillantii*, according to Gruvel, it is still shorter.

New locality. Tasmania, Hobart. On *Pseudocarcinus gigas*, 15. 10. 1904. Pres. by Capt. Francis Mayors.

Distribution. If the association of species proposed in the foregoing is correct, which seems very probable, the species has a very extensive distribution. The question will then be whether local races can be established. Their bathymetrical distribution seems as yet little known.

OCTOLASMIS SESSILIS (Hoek, 1883). (Text-fig. 11.)

Dichelaspis sessilis Hoek, 1883; Weltner, 1922.

The specimen here named *O. sessilis* is particularly defective, internal parts being missing. Besides this species two others are found in the literature which in all likelihood are closely related: *O. hawaiiensis* Pilsbry, 1907 *b* and *O. americanum* Pilsbry, 1907 *a*. Only the external parts of these are described. They may possibly retain their place as species when their internal parts have been described. As regards external parts, only small divergences are found. This specimen agrees well with Hoek's drawings of the species.

Old localities. No. I. Lat. $38^{\circ} 30' N.$, Long. $31^{\circ} 14' W.$, 1829 metres (1000 fathoms). No. II. Lat. $5^{\circ} 24' N.$, Long. $39^{\circ} 19' 8'' E.$, 818 metres (447 fathoms). No. III. Lat. $3^{\circ} 38' S.$, Long. $40^{\circ} 16' E.$, 863 metres (472 fathoms).

Text-figure 11.



Octolasmis sessilis Hoek.

The animal, lateral view.

New locality. Lat. $6^{\circ} 58' S.$, Long. $39^{\circ} 16' E.$, 270 fathoms. (494 m.), 25.9.1911. Pres. by the Eastern and Associated Telegraph Companies.

The species originally known from the Atlantic (No. I.) has thus been re-discovered firstly by the German 'Valdivia' Deep-sea Expedition (1898-99) from the east coast of Africa, in the vicinity of the islands of Zanzibar and Pemba (Nos. II. and III.), and secondly by the finds described above from approximately the same locality. Consequently there should be no doubt that Weltner's specimens are identical with those described above. There is still a great gap to be filled regarding the distribution of this deep-sea species.

Genus MEGALASMA.

MEGALASMA (*GLYPTELASMA*) *HAMATUM* Calman, 1919. (Text-fig. 12.)

Megalasma (*Glyptelasma*) *hamatum* Calman, 1919.

This species, found in the Atlantic as well as from various

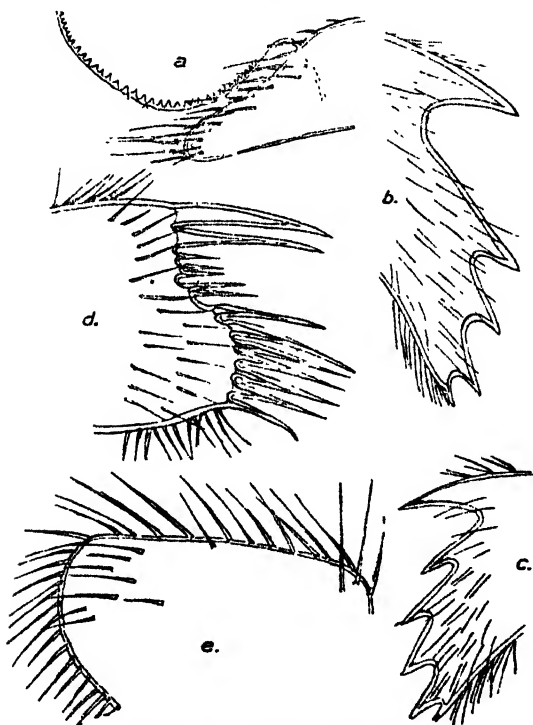
places in the Indian and Pacific Oceans, is easily recognizable internally by a pair of short, hook-like processes on the prosoma and a narrow appendage at the base of the first cirrus. As the species has been described by Calman (1919), only a short complementary description of the mouth-parts and cirri is given here.

Labrum concave, with strong teeth close together.

Palp conical, pointed, with spines along the upper edge and at the point.

Mandible with 4 to 5 teeth and a lower tooth-like angle showing a tendency to division.

Text-figure 12.



Megalasma hamatum Calman.

a. Labrum and palp. b, c. Mandible. d. Maxilla I. e. Maxilla II.

Maxilla I. with an inward curvature with small spines under the upper spines and a projecting part below with stronger spines.

Maxilla II. with straight somewhat convex front edge and straight upper edge. Spines along the whole edge.

As regards the genus *Megalasma*, it can thus be asserted that its mouth-parts correspond very well with the genera *Pacilasma* and *Octolasmis* investigated by the author (1921, tab., p. 139).

Measurements (in millimetres):—







Length of capitulum, 9.5.

Breadth of capitulum, 5.

Length of peduncle, 7.

Breadth of peduncle, 1.5.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	IV.	Caudal appendage.
						
8 10	14 15	16 16	16 16	17 18	17 17	1

The longer *cirri* have five pairs of spines along the front edge of the segments.

Caudal appendage short, one-jointed (fig. 6, Calman, 1919).

Locality. Singapore district. Eastern Extension, Australian and China Telegraph Company.

Genus VERRUCA.

Section *Verruca* Pilsbry, 1916.

VERRUCA CALOTHECA FLAVIDULA Pilsbry, 1916. (Text-fig. 13; Pl. I. fig. 6.)

Verruca calotheca flavidula Pilsbry, 1916.

Complementary description.

With the aid of Pilsbry's good description of this subspecies the specimens at my disposal could be easily identified, so that only a few complementary statements are supplied here.

The *movable plates* had here an evident horizontal position, as Pilsbry states with regard to some specimens.

Broch (1924) devoted some attention to the question of the percentage of individuals with regard to the mobility of the opercular plates of the right or left side, and showed that in a great deal of material about half the individuals had the left side plates movable and half the right side. Of 7 specimens examined here, 4 had the right side opercular plates movable and 3 those of the left side. More material would presumably have shown the same division as Broch found in *V. strömia*, the division appearing to be a matter of chance.

Movable scutum in these specimens with 4 articular ribs under the more or less evidently developed apical rib. The occludent area of the plate with longitudinal ribs divided crosswise by lines of growth as is characteristic of the subspecies. A variation could occur in this respect, 2 specimens having two, 3 specimens three, and 1 specimen four longitudinal ribs. In one case an incipient division of these ridges could be observed.

Movable tergum, according to Pilsbry, as in *V. calotheca*, with four articular ribs. In 6 specimens I found four ridges, in 7 five; thus a less degree of variation occurs here also. *Fixed scutum* and *tergum* as in *V. calotheca*.

Rostrum and *carina* with subequal interlocking ribs. *Rostrum* had, moreover, a scutal area with 5-8 small ribs (in *V. calotheca* two).

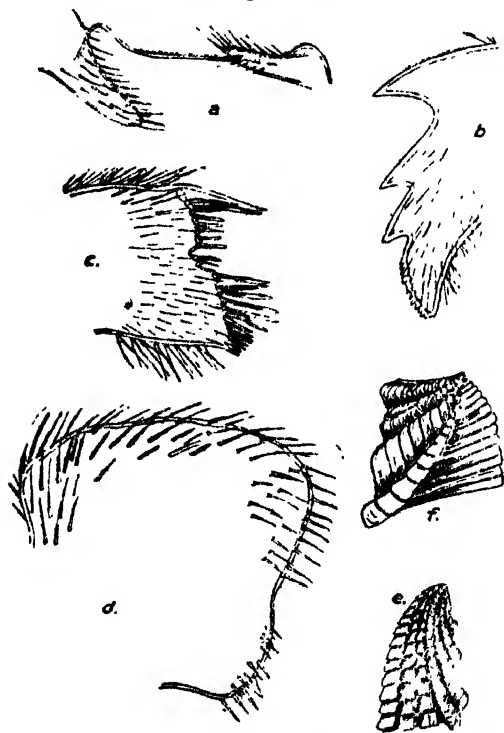
Mouth-parts not previously described.

Labrum slightly concave, with small many-pointed teeth.

Palp conical, with spines along the side and at the point.

Mandible with 3 teeth and a finely-pectinated inner angle. Spines in the younger specimens divided below into two groups.

Text-figure 13.



Verruca calotheca flavidula Pilsbry.

- a. Labrum. b. Mandible. c. Maxilla I. d. Maxilla II. e. Movable scutum.
f. Movable tergum.

Maxilla I. with a notch near the middle of the front edge in the specimens examined. The uppermost spines strongest, lower down smaller. Below the notch, at the top of the projecting part, stronger spines than in the lower angle.

Maxilla II. bilobate, having only a slight notch without spines on the middle of the front edge.

Measurements (in millimetres):—

Carino-rostral length.	Height.
8	7
8	6
8	4

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
11 21	17 23	22 23	28 33	32 35	32 34	20

Cirrus I. with rami differing greatly, *Cirrus II.* with rami differing slightly in length. Remaining cirri with rami of approximately equal length with 4–5 pairs of spines in the front edge of the segments.

The *caudal appendage*, according to Pilsbry, is considerably shorter in *V. calotheca* than in this subspecies. The same number of segments is given in both cases—14 joints. In these specimens the appendages were also long. The number of segments might vary from 17–20 in the same specimen. In one case I found 33 joints.

Old locality. East of Florida.

New locality. St. Vincent—Pernambuco Cable, Lat. 7° 37' S., Long. 34° 26' 5" W., 50–150 fathoms (92–274 m.), 1.6. 1917. Pres. by Eastern and Associated Telegraph Companies.

Section *Rostratoverruca* Broch, 1922.

VERRUCA INTEXTA Pilsbry, 1912. (Text-fig. 14; Pl. I. fig. 7.)

Verruca intexta Pilsbry, 1912.

Discussion.

A few small *Verruca* individuals on an echinoid spine agreed well with Pilsbry's short description of the species *V. intexta*. Allied species are *V. nexa* Darwin, 1854, *V. koehleri* Gruvel, 1907 b, and *V. krügeri* Broch, 1922, which are regarded by Pilsbry (1916) as a "Group of *V. nexa*" of the section *Verruca*, but proposed by Broch as a special section, *Rostratoverruca*, distinguished by its patella-like rostrum, which has arisen through the removal of the umbo from the scutal border. These species are divergent in some minor characteristics. As there has hitherto been but little material of these, it is hard to decide whether variations occur. *V. intexta* and *koehleri* appear to me closely related. An evident difference appears in the number of articular ribs given for the terga and the scuta, three in the former and four in the latter species. *V. krügeri* occupies, according to Broch, a middle position with a varying number of articular ribs (three or four). Moreover, Broch's species diverges by having well-developed ribs which interlock with short ribs on the carina.

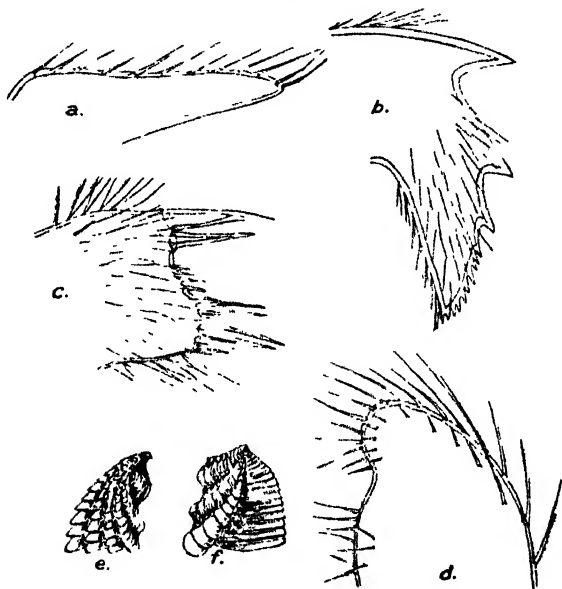
Complementary description.

The species here dealt with, *V. intexta*, has hitherto been but briefly characterized, and has not been figured, wherefore a fuller description with figures is given in the following.

Movable scutum with three articular ribs and three other ribs—in one case four. Scutum somewhat concave inside.

Movable tergum with three articular ribs, including the diagonal rib. No other ribs on the plate. *Fixed scutum* and *tergum* with longitudinal ribs.

Text-figure 14

*Ferruca intexta* Pilsbry.

- a. Palpus. b. Mandible. c. Maxilla I. d. Maxilla II. e. Movable scutum.
f. Movable tergum.

Carina with ribs which interlock with those of the rostrum. On the other hand, there are not, as in *V. krügeri* Broch, 1922, ribs towards the tergum, as the latter has no longitudinal ribs towards the carina. The ribs of the carina towards the rostrum are of the same size in these specimens. According to Pilsbry's description, the uppermost is the largest ("longer than the others"). In *V. koschleri*, which most resembles *intexta*, the middle rib is largest. Maybe this has no great systematic importance, since it is merely a quantitative property. The umbo in these specimens is somewhat produced, as Pilsbry also states.

Rostrum patella-shaped because of the umbo being removed

from the apex. From the umbo there proceed numerous ribs, some of them alternating with those of the scutum and carina.

Basal edges of the plates not inflexed as in *V. nexa*.

Mouth-parts not previously described.

Labrum somewhat concave, with teeth.

Palp conical, pointed, with spines along one edge.

Mandible with three teeth and the lower part of the front edge finely pectinated.







Maxilla I. with strong upper spines and an excavation underneath with smaller spines. Under that a projecting portion with larger spines.

Maxilla II. evidently bilobate.

Measurements (in millimetres):—

Carino-rostral diameter, 4; height, 1.5.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
						
12 18	8 15	17 18	19 20	— 25	27 27	15

The first two *cirri* with rami very unequal in length. The other with rami of approximately equal length with 3 pairs of spines on the front edge of the segment.

Caudal appendage about one-third the length of cirrus VI., with 11 and 15 segments respectively in the specimen examined.

Old locality. Philippines, off N.W. Panay, 312 fathoms (571 m.).

New locality. E. of Madagascar, Saya de Malha bank, 150 fathoms (275 m.). Pres. by Prof. Stanley Gardiner.

Section *Altiverruca* Pilsbry, 1916.

VERRUCA RATHBUNIANA Pilsbry, 1916. (Text-fig. 15.)

Verruca rathbuniana Pilsbry, 1916.

Complementary description.

This species is represented here by a single specimen. Many species are brought under section *Altiverruca*, often diverging from each other in smaller characteristics as, for example, number of articular ribs on the movable scutum and tergum, and the number of interlocking teeth between the rostrum and carina. In the latter character it seems to me that *V. rathbuniana* and *quadrangularis* Hoek, 1883 closely agree, since the carino-rostral suture has two interlocking teeth. There is resemblance in other respects also. Further finds are, however, necessary to decide whether there are one or two species here. As regards externals, see Pilsbry's description (1916). There it is stated (p. 42): "The rostrum is higher than the carina." Here is a printer's error, for it must really be the contrary. For comparison, figures of rostrum and carina are given (text-fig. 15, *e, f*). The same also appears from Pilsbry's fig. 2, pl. vii.

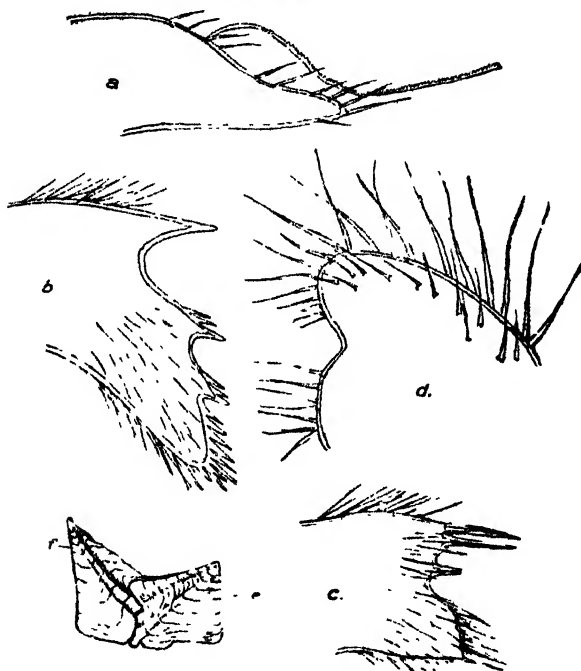
Mouth-parts not previously described.

Labrum concave, with small close-growing teeth.

Palp conical, pointed, with spines along one edge.

Mandible with 3 teeth and a pectinated lower angle. Tooth 2 and 3 with additional teeth. This mouth-part agrees very well with that of *V. quadrangularis*, which, according to Hoek's figure, is provided with additional teeth on the third tooth.

Text-figure 15.



Verruca rathbuniana Pilsbry.

a. Labrum. b. Mandible. c. Maxilla I. d. Maxilla II. e. Rostrum. f. Carina.

Maxilla I. with evident notch on the middle. Above this, and adjacent, some small spines and at the top larger ones. Inner angle projecting with strong spines. This mouth-part resembles also to some extent that of *V. quadrangularis*.

Maxilla II. bilobate, with notch without spines and of the usual appearance of *Verruca*.

Measurements (in millimetres):—

Carino-rostral length, 5; height, 3.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
9 10	6 11	15 16	19 20	— 20	19 20	8

Cirrus I. with rami of nearly equal length.

Cirrus II. with rami slightly unequal in length and the other cirri with rami of fairly equal length. The number of segments also agrees well with the statements of Pilsbry. *Cirrus I.*, according to Pilsbry, with 10 and 11, *cirrus II.* with 6 and 11 segments. These statements apparently refer to somewhat larger individuals than those examined here. *V. quadrangularis* appears also to have an approximately equal number of segments: according to Hoek *cirrus I.* with 7 and 10, *cirrus II.* with 7 and 9, *cirrus III.* with 14 and 15 segments.

Caudal appendage in Pilsbry's specimen broken off, but stated to be short. In this specimen it is somewhat shorter than the protopodite and with 8 segments, this being the same as Hoek gives for *V. quadrangularis*.

Old locality. S.E. of Cape Cod, Lat. 40° 29' N.; Long. 66° 4' W., 1769 fathoms (3237 m.).

New locality. Between Santiago and St. Vincent (Cape Verde Islands), 990 fathoms (1812 m.), 19. 1. 1919. Pres. by Eastern and Associated Telegraph Companies.

VERRUCA NAVICULA Hoek, 1913. (Text-fig. 16; Pl. I. figs. 8-12.)

Verruca navicula Hoek, 1913.

Complementary description.

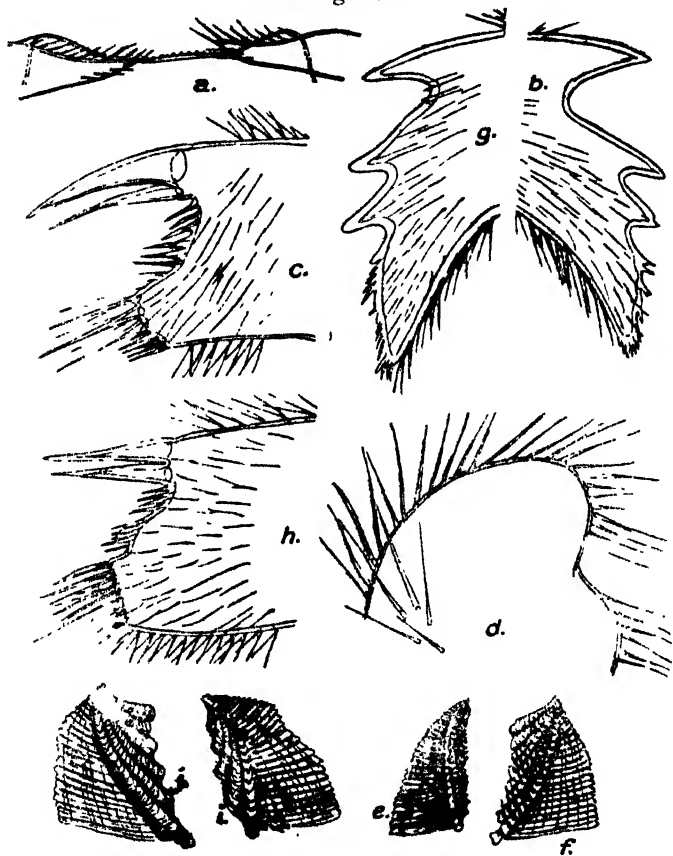
This material contained 6 individuals of this species from two localities in the Java Sea and one specimen from the ocean west of New Zealand, all from a great depth. The species was fully described by Hoek (1913) from two individuals. As there are 7 specimens here, the examination of Hoek's description will be chiefly confined to the establishment of eventual variation.

In both of Hoek's specimens the *opercular plates* of the left side were movable. Of these specimens the opercular plates of 4 were movable on the right side and 3 on the left. This species is most easily recognizable by the opercular plates. Hoek (1913, p. 137) says: "This is a very characteristic species. It is recognizable at once by the height of the movable tergum and scutum and the numerous ridges, which serve for the articulation of these valves." It is an interesting study to ascertain whether the articular ribs in this species are fixed in number, which is often the case in other *Verruca* species. Hoek gives for the movable scutum 5 articular ribs (the axial ridge included); for the movable tergum 6. The following summary of the number of ridges in the present specimens will indicate the prevalence of some variation:—

Localities.	Movable scutum.	Movable tergum.
Java Sea.....	6	8
	5	6
	6	7
	7	7
	6	6
	6	6
W. of New Zealand.	5	6

In certain cases also one can see how a rib begins to be divided into two. In any case the great number of ribs is a distinguishing mark of the species. As regards the opercular plates, I find good

Text-figure 16.

*Verruca navicula* Hoek.

Individuum from Java Sea :—a. Labrum and palpus. b. Mandible. c. Maxilla I.
d. Maxilla II. e. Movable scutum. f. Movable tergum.

Individuum from Pacific Ocean between Australia and New Zealand :—g. Mandible.
h. Maxilla I. i. Movable scutum. j. Movable tergum.

agreement with the statements of Hoek. In one case, the specimen from New Zealand, the tergum was not so regularly quadrangular, as the longer of the occludent margins is somewhat irregular, this being connected with the divergent manner of growth of this individual. For comparison with Hoek's figure

I give here a figure of two individuals from widely-separated localities (text-fig. 16), likewise a photograph (Pl. I. figs. 8-12).

There occurred on the carina of all the specimens the distinct furrow, running at some distance from the tergal margin towards the apex of the valve, in which the rostrum is inserted. As regards the development of the ribs there is a slight variation; they can be more or less evident, as will appear from the photos. For the rest, I refer to Hoek's description.

The *fixed scutum* and *tergum* are also in agreement with Hoek's specimens, as appears from Pl. I. fig. 11. The lines of growth as well as the vertical folds mentioned by Hoek was here very evident. In the specimens from New Zealand both plates were not straight, but slightly bent outwards, this being connected with the above-mentioned divergent manner of growth in this individual.

The base in all these specimens were membranous. Hoek indicated this with some doubt.

Mouth-parts fully described and partially drawn by Hoek. For comparison, figures are given here of the specimen from the Java Sea and one from New Zealand showing evident resemblance to those of Hoek.

Measurements (in millimetres):—

Localities.	Nos.	Carinal-rostral diameter.	Height.
Java Sea.....	1	10	9
Java Sea	2	12	12.5
W. of New Zealand ...	3	14	9

Number of segments in the Cirri:—

Localities.	Nos.	I.	II.	III.	IV.	V.	VI.	Caudal appendage.
Java Sea ...	1	12 24	8 22	22 25	28 29	30 34	33 34	39
Java Sea	2	14 28	10 27	26 28	30 35	34 35	37 38	38
West of New Zealand ...	3	13 27	10 25	9 32	34 38	36 39	41 44	41

Cirrus I. and *II.* with rami of very unequal length, as stated by Hoek. As these specimens were larger than those of Hoek, more segments were obtained on the rami. For cirrus VI. Hoek gives 23-24 segments; in these there were 33-44 segments.

The *caudal appendage* I find equal in length to more than half of cirrus VI. and with numerous segments.

Old localities. Malay Archipelago between Flores and Sumba and between New Guinea and Ceram, 1691-1755 fathoms (924-959 m.).

New localities. No. 1. The Java Sea, Lat. 9° 6' S., Long. 115° 10' E., 1500 fathoms (2745 m.), 29. 3. 1916. Pres. by Eastern and Associated Telegraph Companies. No. 2. The Java Sea, Lat. 9° 16' S., Long. 117° 1' 35" E., 1380 fathoms (2525 m.), 16. 7. 1907.

Pres. by Dr. F. Wood Jones. No. 3. Pacific Ocean, Lat 37° S., Long. 163° 30' E., 1500 fathoms (2745 m.), 6. 3. 1918. Pres. by Eastern and Associated Telegraph Companies.

Genus CUTHAMALUS.

CUTHAMALUS CHALLENGERI Hoek, 1883. (Pl. I. fig. 13.)

Syn. Author, 1921.

This species, found previously several times in the Japanese Sea, is here represented by a collection of large individuals up to 9.5 millimetres in carino-rostral length, residing on a *Mytilus* individual.

New locality. Japan, Hakodadi.

Distribution. Japanese and Malayan waters.

CUTHAMALUS ANTENNATUS Darwin, 1854.

Syn. Author, 1921.

This species is represented by an individual attached to a stone. Though the material was dry, an examination of the internal parts was possible, at which the antenna-like ramus on cirrus III. which is characteristic of some individuals of this species was met with. Description by the Author, 1921, '26; Broch, 1922.

New locality. New South Wales, Jervis Bay, Huskinson, from between tide-levels, 1925. Pres. by F. A. Rodway.

Genus PACHYLASMA.

PACHYLASMA SCUTISTRIATA Broch, 1922. (Text-fig. 17; Pl. I. fig. 14.)

Pachylasma scutistriata Broch, 1922.

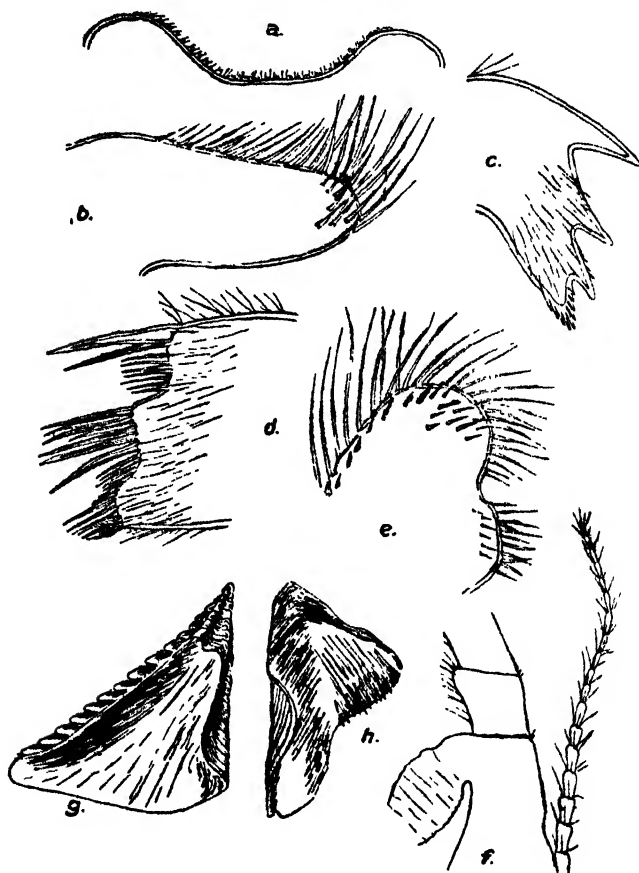
Complementary description.

Up to the present only six species of this genus have been described. Notwithstanding the small number of species, considerable difficulty prevails as to the determination of forms. These specimens from two localities seem at first sight to agree with *P. crinoidophilum* Pilsbry, 1911 from Kagoshima Gulf, which species, however, diverges in some characters, *e. g.* the width of the carino-lateral compartments. In Broch's species, as well as in these individuals, the lateral and carino-lateral compartments are of the same width. A certain resemblance also exists between the specimens and *P. giganteum* Darwin, 1854, known from the Mediterranean. The species appears, however, to diverge in the matter of the opercular plates. These individuals agree best with Broch's *P. scutistriata* from Bass Strait, Australia. For comparison a photo of the outer parts is given. According to Broch the *basis* is membranous in young specimens,

in older ones calcified. These specimens all had an evidently calcified base. *Scutum* and *tergum* agree with Broch's figures.

Mouth-parts. Labrum, according to Broch, without hair and teeth. In one specimen I found hair, in another also many-pointed teeth.

Text-figure 17.



Pachylasma scutistriata Broch.

a. Labrum. b. Palpus. c. Mandible. d. Maxilla I. e. Maxilla II. f. Cirrus VI. and caudal appendage. g. Scutum. h. Tergum.

Palpus conical, with spines in the front part and along the upper edge.

Mandible and *Maxilla I.* as in Broch's specimens.

Maxilla II. evidently bilobate, with inward curvature on the middle, of the appearance typical to the family Chthamalidae.

Measurements (in millimetres):—

	Carino-rostral length.	Height.
Largest specimens	31	26
Smallest specimens	14	13

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.	Caudal appendage.
11 13	14 20	20 20	27 27	28 30	30 31	18
9 12	16 18	22 22	24 27	27 28	30 33	19

Like Broch, I find in these specimens long *caudal appendages*, these also being found in *P. giganteum*.

Whether these two species are clearly divergent cannot at present be decided, as further finds of *P. giganteum* are lacking. It seems odd that the character to which great weight has been attached in distinguishing the *Pachylasma* species (the width of the lateral and carino-lateral compartments) according to Darwin (1854, p. 478) can be liable to variation connected with different stages of development. There would then be the same uncertainty with regard to other species, and, in that case, the whole genus should be subjected to revision.

Old localities. Between Tasmania and Australia.

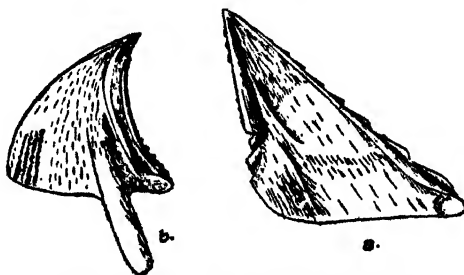
New localities. Lat. 8° 46' S., Long. 114° 44' E., 400 fathoms (732 m.), 28.7. Pres. by Eastern Telegraph Company.— Lat. 6° 15' N., Long. 93° 35' E., S.E. of Great Nicobar, 1040–1120 fathoms (1903–2050 m.), 30.4.1925. Pres. by Eastern Extension Telegraph Company.

Genus *BALANUS*.Subgenus *MEGABALANUS* Hoek, 1913.

BALANUS TINTINNABULUM PENINSULARIS Pilsbry, 1916. (Text-fig. 18.)

Balanus tintinnabulum peninsularis Pilsbry, 1916.

Text-figure 18.



Balanus tintinnabulum peninsularis Pilsbry.

a. Scutum. b. Tergum.

These specimens from Japan agreed well with the subspecies of Pilsbry described from California. Inner parts were lacking. In outer parts complete resemblance through the close-growing spines of parietes. The plates were beautifully rose-coloured. Scutum and tergum (text-fig. 18) agree well with Pilsbry's figures.

Measurements (in millimetres):—

Carino-rostral length.	Height.
13	12
18	19
43	40

The allied *B. tintinnabulum spinosus* (Gmelin) has more strongly-developed spines on parietes.

Old locality. Lower California, Cape St. Lucas.

New locality. Japan, Sagami, Misaki, 25. 12. 1921. Pres. by Alan V. Insole.

BALANUS DECORUS Darwin, 1854.

Balanus decorus Darwin, 1854; Hutton, 1879; Gruvel, 1905; Chilton, 1909; Pilsbry, 1916; Jennings, 1918; Withers, 1924.

Balanus amphitrite communis Borradaile, 1916.

Locality. New Zealand, Hauraki Gulf, 5. 11. 1912.

Subgenus *BALANUS* Da Costa.

BALANUS TRIGONUS Darwin, 1854.

These specimens are derived from the same locality as some of Broch's (1922). As I discussed in 1921 the dental armature of cirrus III. in specimens from Japan and the W. Indies, it is deserving of mention here that the specimen had strong teeth on the front edge of the segment of cirrus III.

Locality. New Zealand, Hauraki Gulf, 5. 11. 1912.

BALANUS SPONGICOLA Brown, 1827.

Balanus spongicola Brown, 1827, 1844; Darwin, 1854; Gruvel, 1905, 1907 a, 1909, 1910, 1920; Stebbing, 1910; Pilsbry, 1916; Barnard, 1924.

This species, fully described by Pilsbry, is represented here by 4 specimens. By comparison I am able to establish resemblance in the outer parts to Darwin's specimens. The plates and inner parts agreed well with former descriptions.

Size of the largest specimen (in millimetres):—

Carino-rostral length, 19; height, 15.

The species found in numerous localities in different parts of the world appears to be cosmopolitan in its distribution.

New locality. Off cable between Pai and Maricas Island, Rio de Janeiro.

Subgenus *HESPERIBALANUS** Pilsbry, 1916.*BALANUS HESPERIUS* forma *LAVIDOMUS* Pilsbry, 1916.*Balanus hesperius laavidomus* Pilsbry, 1916.

Balanus hesperius with forma *laavidomus* was described as late as 1916. The species, however, is not rare along the coasts of the Pacific. In the collection of the British Museum, I found 3 specimens which agreed well with the forma *laavidomus*, which in typical cases has the external wall smooth.

Measurements (in millimetres) :—

Carino-rostral length, 13; height, 6.

For the rest I refer to the figures and descriptions of Pilsbry.

Locality. Fort Rupert, Vancouver Island.

Distribution. Monterey, California to Alaska.

BALANUS TENUIS Hoek, 1883.

Syn. Author, 1925; Barnard, 1924.

These particularly defective specimens without opercular plates and inner parts I believe I can bring under *B. tenuis*, which I had previously had the opportunity of examining (the Author, 1925).

New locality. Java Sea, Lat. 7° 35' S., Long. 114° 30' 30' E., 73–175 fathoms (134–320 m.), 28. 7. 1917. Pres. by Eastern and Associated Telegraph Companies.

Distribution. Pacific Ocean, E. and S. of Japan; E. and S. China Sea; Philippine Archipelago; Java Sea.

Subgenus *CHIRONA* Gray, 1835.

BALANUS AMARYLLIS Darwin, 1854,²forma *EUAMARYLLIS* Broch, 1922.

Syn. Author, 1921.

These specimens were all typical *B. amaryllis*. Inner parts showed great resemblance to former descriptions. Broch states that in forma *eu-amaryllis* cirrus VI. sometimes has 3–4 pairs of spines on the front edge of the segments. In these specimens, however, I find the number of anterior spines given by Darwin, viz. 2 pairs. The carino-rostral length of the largest specimen was 30 mm. and the height 35 mm., which is somewhat less than what Darwin gives for his largest specimen.

Locality. Java Sea, 16. 10. 1906. Pres. by Francis Worsley.

* To the same subgenus (*Hesperibalanus*) Barnard refers a new species, *B. elisabethæ* from South Africa, which is stated to be closely allied to *B. hesperius nipponense*. Figures are unfortunately lacking.

Genus *ELMINIUS*.*ELMINIUS MODESTUS* Darwin, 1854.

A few small specimens of this species were found on algæ. The plates had two folds, which I have also found in younger specimens of the species (Author, 1926). In full-grown specimens these folds are divided into several.

Locality. New Zealand, Hauraki Gulf, 5. 11. 1912.

Genus *TETRACLITA*.Subgenus *TETRACLITA*.*TETRACLITA POROSA JAPONICA* Pilsbry, 1916.

Syn. Pilsbry, 1916.

This subspecies is, according to Pilsbry, the prevalent form of the species in Japan. These three specimens agreed well with regard to the opercular plates with those of Pilsbry in that the scutum had in the inflected occludent border few strong teeth (in these 3, in Pilsbry's 4 or 5). In *Tetracrita porosa viridis*, on the other hand, numerous small teeth are found. The spur also small, as stated by Pilsbry.

Locality. Japan, Sagami. Misaki, 23. 12. 1921. Pres. by Alan V. Insole.

TETRACLITA POROSA STALACTIFERA (Lamarck).

Syn. Pilsbry, 1916.

Some dry specimens of *Tetracrita* from Pernambuco agree well with the subspecies fully described and figured by Pilsbry. Darwin's var. *communis*, which is put by Pilsbry in this subspecies, was found at Pernambuco, the same locality as the specimens dealt with here.

Locality. Off reef at Pernambuco. Pres. by Sir David Wilson Barker.

Subgenus *TESSEROPORA* Pilsbry, 1916.*TETRACLITA (TESSEROPORA) ROSEA* (Krauss, 1848).

Conia rosea Krauss, 1848, Darwin, 1854; Gruvel, 1905; Stebbing, 1910; Pilsbry, 1916; Barnard, 1924.

Complementary description.

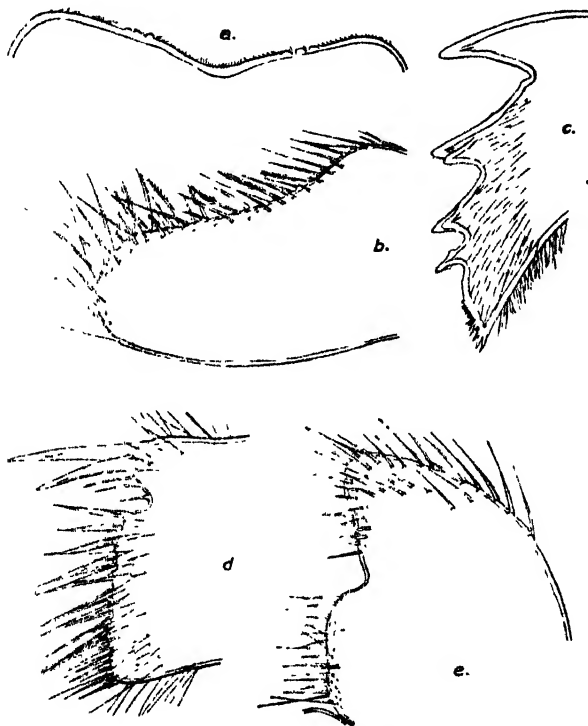
The species is represented in the material of the British Museum by some dry specimens, of which the smaller had a smooth shell, the larger a creased one of the appearance shown by Darwin's pl. x. fig. 3 (1854). The species, whose outer parts are easily recognizable, is very briefly described as to its inner parts. As yet another species of the subgenus *Tesseropora* has become known, viz. *Tetracrita wireni*, mihi, 1921, which has been fully described as to its inner parts. I will give for comparison some information about the mouth-parts and cirri.

Although the specimens were dry, I succeeded by the use of alcohol and glycerine in softening the animals so that preparations of mouth-parts and cirri could be made.

Mouth-parts afford very great resemblance to the kindred above-mentioned species.

Labrum with a slight inward flexion at the middle. On each side 3 strong teeth. Along the whole edge fine hair.

Text-figure 19.



Tetracilita rosea Krauss.

a. Labrum. b. Palpus. c. Mandible. d. Maxilla I. e. Maxilla II.

Palp long, not pointed at the front, but rounded. Upper edge concave, lower edge convex. Spines at the end and along the upper edge. Some of these strongly feathered.

Mandible with 4 strong teeth and a somewhat pectinated region on the front edge below. Some additional teeth can be found on teeth 2-4.

Maxilla I. with straight front edge with marked inner angle. Plain notch in the upper part of the front edge. The spines situated above that strongest.

Maxilla II. rather wide; wider than in *T. wireni*. Notch without spines on the middle of the front edge.

Measurements (in millimetres):—

Carino-rostral length, 22; height, 10.

Number of segments of the Cirri:—

I.	II.	III.	IV.	V.	VI.
10 20	13 20	17 24	20 21	— 23	— 25

Cirri I. and *II.* with rami of unequal length; *cirrus III.* with rami of almost equal length. In *T. wireni*, mihi, cirri II. and III. had rami of the same length. Further finds should make it clear whether this difference has any significance. In other species, as, for instance, *T. serrata*, great variations in the length of the cirri are found.

The longer cirri had three pairs of spines on the front edge of each segment.

New locality. New South Wales, between tide-marks at entrance to Shoalhaven River. Pres. by F. A. Rodway.

Distribution. Australia, S. Africa.

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EXPLANATION OF THE PLATE.

- Fig. 1. *Lepas anatifera nonfurcata*, var. n. $\times 0\cdot87$.
2. *Heteralepas japonica* f. *indica*. Locality no. 4. $\times 1$.
3. *Heteralepas japonica* f. *indica*. Locality no. 5. $\times 0\cdot95$.
4. *Heteralepas japonica* f. *indica*. Locality no. 9. $\times 0\cdot86$.
5. *Heteralepas lankesteri* Gruvel, 1900. $\times 0\cdot87$.
6. *Verruca calotheca flavidula* Pilsbry, 1916. $\times 1$.
7. *Verruca intertexta* Pilsbry, 1912. $\times 1\cdot23$.
8. *Verruca navicula* Hoek, 1913. Locality no. 1. $\times 1\cdot2$.
- Figs. 9, 10, 11. *Verruca navicula* Hoek, 1913. Locality no. 2. $\times 0\cdot86$.
- Fig. 12. *Verruca navicula* Hoek, 1913. Locality no. 3. $\times 1$.
13. *Chthamalus challengerii* Hoek, 1883. $\times 1$.
14. *Pachylasma scutistriata* Broch, 1922. $\times 0\cdot95$.

EXHIBITIONS AND NOTICES.**May 10th, 1927.**

Major S. S. FLOWER, O.B.E., Vice-President,
in the Chair.

Mr. D. SETH-SMITH, Curator of Mammals and Birds, exhibited a series of living specimens of the following species of Lovebirds in the Society's collection : --

Agapornis cana.

- " *pullaria.*
- " *roseicollis.*
- " *taranta.*
- " *nigrigenis.*
- " *liliane.*
- " *personata.*

Mr. R. I. POCKOCK, F.R.S., exhibited the skin of a remarkable variety of Leopard procured from a native in the southern part of the province of Kanara, South India, by Mr. C. A. Souter, I.C.S., who had deposited it in the Natural History Museum, S. Kensington. The skin differs from that of normal Indian leopards in the modification of the pattern.

The ordinary rosettes are broken up and fused to such an extent that, supplemented with additional pigment, they convey the impression of a blackish animal speckled and streaked with yellow. From the crown of the head to the root of the tail runs a broad black band, which, on the shoulders and posterior half of the back, is defined laterally by yellow streaks of varying length arranged subsymmetrically in two longitudinal broken lines. Over the withers this band is very distinctly speckled with yellow; on the nape and fore part of the back it is at most faintly speckled, whereas on the posterior part of the back it is marked with narrow, indistinct, pale longitudinal streaks. The spotting on the top and sides of the head and on the neck is more normal, but the spots are to a great extent confluent. The fore legs are thickly and closely spotted to the feet, the spots becoming more and more coalesced into interlacing lines up towards the withers. On the flanks the spots similarly run together into irregular zigzag interlacing lines defining streaks and spots of yellow or fawn. On the thighs the spots flow together into larger black blotches, relieved by pale spots and streaks, the latter in some cases being comparable to forked lightning. The hind legs are spotted to the feet, but not so closely as the fore legs. The tail is mostly black along its upper side, but streaked with yellow on its basal half. The lower parts are white as in ordinary leopards, and the spots apparently run

into abbreviated black lines, but a good deal of the skin of this area has been cut away in the making of it into a rug.

So far as Indian leopards are concerned, this variety most.

Text-figure 1.



Variety of Leopard from Kanara, S. India.

nearly resembles one shot by Mr. F. A. Coleridge at Putnam in Cuddapah, the skin of which was exhibited by Mr. Lydekker at the Zoological Society and described and figured in the Society's

'Proceedings,' 1908, pt. 1, pp. 1-3, text-fig. 1. In this skin, judging from the photograph, the normal rosettes on the body are mostly partially broken up and coalesced into patches or blotches of irregular shape, simulating very large rosettes, each of which is wholly or partly margined with a black line surrounding a darker area dotted with more or fewer solid spots. Here and there the spots run together into black streaks. The blotches, especially on the flanks, are separated and sharply defined by a large-meshed network of narrow yellow lines; but on the dorsal area the blotches fuse to a greater or less extent to form a broad blackish band extending from between the ears to the root of the tail and defined laterally by a narrow yellow branching longitudinal streak. Anteriorly this dark band is somewhat diamond-shaped, being pointed on the crown, angularly expanded on the nape of the neck, and constricted behind over the shoulders, where the yellow streaks which define it curve outwards or downwards towards the elbow and are not continuous with the yellow streak, sometimes interrupted, which defines the dark band on the back and loins. The face, the sides of the neck and the limbs are heavily but more normally spotted, and the upper side of the tail is blackish, speckled with yellow. An interesting point about this skin is that it holds a nearly intermediate position between the skins of normally coloured leopards and Mr. Souter's skin from South Kanara. The latter, however, has progressed a stage further in the direction of this peculiar method of nigrescence attained by the disintegration and coalescence of the rosettes, a method which is quite distinct from that of ordinary black leopards, where the blackness is due to the pigmentation of the pale areas obscuring the normal rosettes, which are typically only visible under reflected light.

The method exhibited by the skin from Kanara is precisely similar to that of some leopards recorded from the neighbourhood of Grahamstown in South Africa, to which Dr. Günther gave the name *Felis pardus melanotica* (Proc. Zool. Soc. 1885, p. 243, pl. xvi.). In the first specimen of this mutation to come to hand the rosettes were broken up into a multitude of small black spots, thickly covering the body and confluent for the most part all over the flanks, and especially in the middle of the back, which is black. But in a second much darker skin received in the following year and also described by Dr. Günther (Proc. Zool. Soc. 1886, p. 203), the back, flanks, upper side of the tail, nape of the neck, and crown of the head are practically black all over, except for some normally-coloured patches in front of and behind the shoulders, the sides of the neck, the throat and belly remaining white with black spots, the outside of the fore limbs and of the hind limbs below the hocks being thickly marked with small spots and the thighs blotched with larger more or less confluent spots. A photograph of this skin, preserved in the British Museum, is here reproduced for comparison with the skin from

Southern Kanara. It clearly represents a further stage of the nigrescence exhibited by the Indian skin; but what appears to be a still blacker example is preserved in the South African Museum at Cape Town and was figured by Mr. W. L. Selater in 1900 ('The Fauna of South Africa: Mammals,' vol. i. p. 36,

Text-figure 2.



Variety of Leopard from Grahamstown, S. Africa.

fig. 10). This specimen, judging from the figure, is only definitely spotted on the sides of the neck, on the fore paws, and on the hind legs below the hocks. Especially does it differ apparently from the skin from Grahamstown, here figured, in having the cheeks, throat, belly, inside of the limbs, and underside of the tail black,

like the back and flanks. But possibly the darkness of these areas is due to shadow. Mr. Sclater did not describe the specimen or comment on any differences between it and the examples recorded by Dr. Günther.

A further point of interest connected with Mr. Souter's skin from South Kanara is the proof it affords of the occurrence in Indian Leopards of the type of nigrescence hitherto believed to be found only in African specimens, and it now remains to be seen if the black leopards referred to by Blanford ('Fauna of British India: Mammalia,' p. 69, 1888) as commoner in the hills of Southern India and in Travancore than elsewhere in Peninsular India are of the ordinary kind which is mostly imported from the countries to the east of the Bay of Bengal or to the kind typified by the Grahamstown variety.

Mr. G. C. ROBSON, M.A., F.Z.S., exhibited a series of lantern-slides and specimens illustrating (a) a special type of *Hectocotylus* in the Octopoda and (b) a reconsideration of the function of the *Hectocotylus*.

May 24th, 1927.

Major S. S. FLOWER, O.B.E., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of April 1927:—

The registered additions to the Society's Menagerie during the month of April were 187 in number. Of these 25 were acquired by presentation, 124 were purchased, 6 were received in exchange, and 32 were born in the Menagerie.

The following may be specially mentioned:—

2 Trinidad Motmots (*Momotus swainsoni*), new to the Collection, presented by Miss Byatt on April 18th.

1 Brown-necked Parrot (*Paecephalus fuscicollis*), from Northern Rhodesia, presented by Mr. W. Singleton Fisher on April 30th.

Mr. R. H. BURNE, M.A., F.R.S., F.Z.S., exhibited, and made remarks upon, injected preparations from the Angler-fish and the Cod, showing the presence and distribution of vessels of unknown function related to the lymphatic system.

June 7th, 1927.

Prof. E. W. MACBRIDE, M.A., D.Sc., F.R.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of May 1927:—

The registered additions to the Society's Menagerie during the month of May were 203 in number. Of these 67 were acquired by presentation, 112 were purchased, 1 was deposited, and 23 were born in the Menagerie.

The following may be specially mentioned:—

A Greater Bird-of-Paradise (*Paradisea apoda*) and a Black-headed Butcher-Crow (*Cracticus cassicus*) from the Aru Islands, presented by Alfred Ezra, O.B.E., F.Z.S., on May 13th.

A Violaceous Plantain-eater (*Musophaga violacea*), a Crowned Duiker (*Sylvicapra coronata*), and several other mammals and birds, from Northern Territories, Gold Coast, presented by A. W. J. Pomeroy on May 21st.

Prof. J. P. HILL, F.R.S., F.Z.S., exhibited, and made remarks upon, a remarkable series of photographs and drawings of *Echidna* and *Ornithorhynchus* Embryos.

Dr. H. H. SCOTT, F.Z.S., exhibited, and made remarks upon, the Crop contents of two Ostriches.

Prof. W. ROWAN exhibited, and made remarks upon, a series of photographs bearing on the problem of Bird Migration.

Mr. D. SETH-SMITH, F.Z.S., gave an account of the Birds he had seen during visits to the Society's new Estate at Whipsnade.

[‘Proceedings,’ 1927, Part II. (pp. 258–490), was published on July 10th, 1927.]



ETHIOPIA POTENZIALI LIBERI



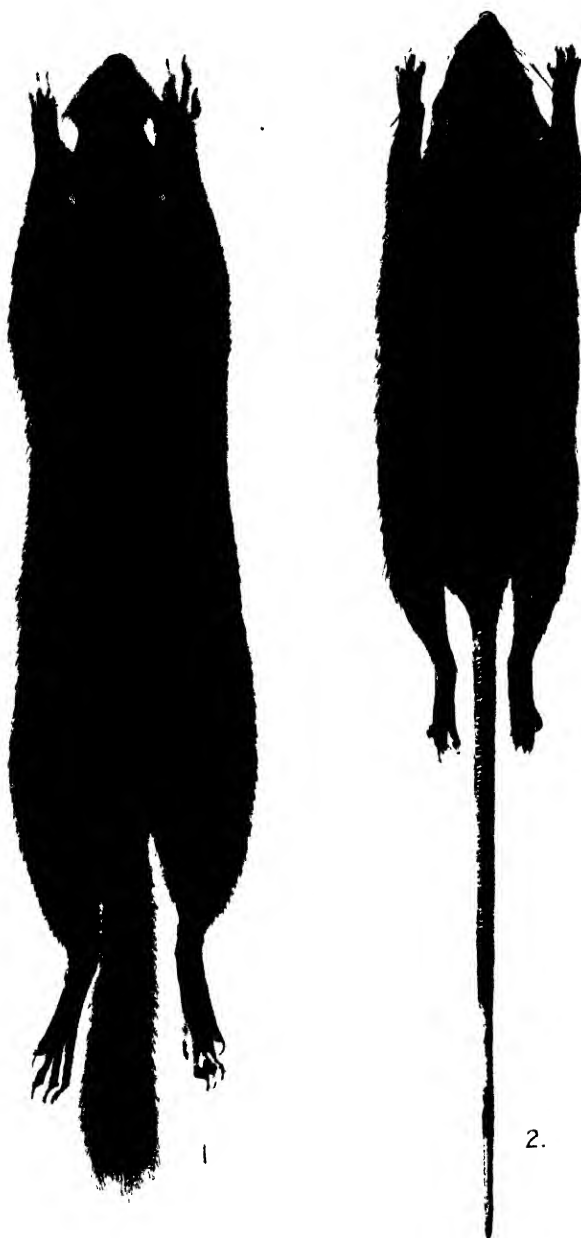
SIMIAS CONCOLOR SIBERU



Sciurus

Sciurus

1 SCIURUS MELANOGASTER MENTAWI 2 S MELANOGASTER MELANOGASTER
3. S MELANOGASTER ATRATUS.



2771

John Bale Chasen & Danielsson, U

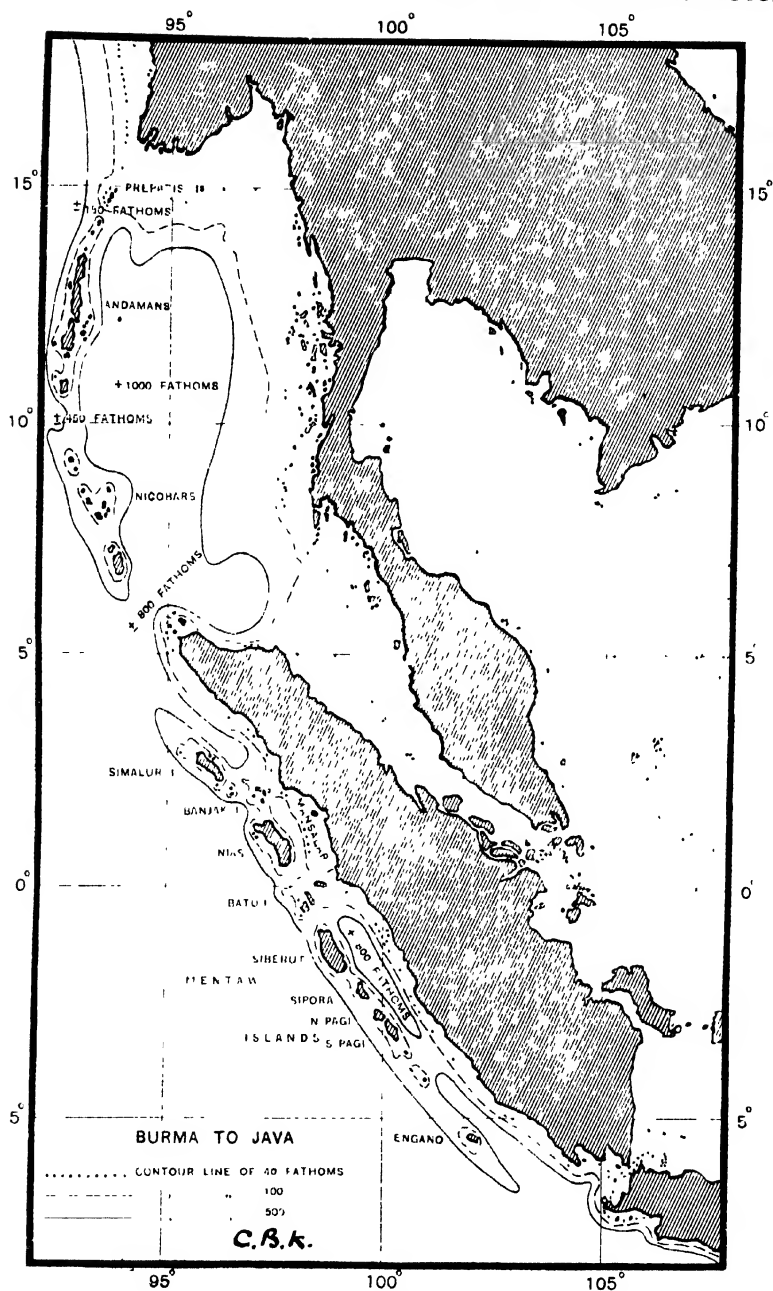
1 LARISCUS NIOBE SIBERU. 2 RATTUS SABANUS SIPORANUS $\frac{1}{4}$ nat size



1.



2.



41. Spolia Mentawiensia.—Mammals. By F. N. CHASEN, C.M.Z.S., and C. BODEN KLOSS, F.Z.S. With an Introduction by C. BODEN KLOSS.

[Received July 30, 1927 Read November 16, 1927.]

(Plates I. V. and Map *.)

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I INTRODUCTION.

The Mentawi Group, to the west of Sumatra, consists of the islands of Siberut, Sipora, and North and South Pagai. The first and northernmost, roughly quadrilateral, about sixty geographical miles long and twenty-five wide, is larger than the other three (which are fairly equal in size) put together—there are also a number of small islands near their shores. The group lies parallel to the coast of Sumatra and about fifty to eighty miles distant; its northern extremity is Lat. 1° South.

The mammals of Sipora Island had been collected by Dr. E. Modigliani in 1892, and those of the Pagai Islands by Dr. W. L. Abbott and myself in 1902; but Siberut had never been worked by a naturalist until I landed there in September 1924, accompanied by Mr. N. Smedley, Assistant Curator of the Raffles Museum, Singapore, and a party of native assistants. I had several times since the visit to the Pagai Islands applied to the Government of Netherlands India for permission to visit Siberut, but sanction had been withheld on account of the attitude of the Indonesian inhabitants, the last in the group to come under administration. At length, in 1923, however, the Government was able to agree to a visit, and when the time came a year later to make it, gave assistance, as usual, in a most generous manner. A month was spent on Siberut (Sept.-Oct.) and another on Sipora (Oct.-Nov.), and besides obtaining much zoological material, both vertebrate and invertebrate, collections of plants and ethnographical objects were made as well. Reports on all these, as prepared, are being published under the general title 'Spolia Mentawiensia.' The following have already appeared:—

- i. The Flora of the Mentawi Islands. H. N. Ridley, Kew Bulletin, 1926, pp. 56-94.

* For explanation of the Plates, see page 840.

- ii. Birds. F. N. Chasen and C. Boden Kloss, *Ibis*, 1926, pp. 269-306, pl. iii. and map.
- iii. Reptiles and Amphibians. Malcolm A. Smith, *Ann. Mag. Nat. Hist.* (9) 1926, xviii. pp. 76-81.
- iv. Zoraptera. H. H. Karny, *Treubia*, ix. 1926, pp. 1-5, pl. i. text-figs. 1-3.
- v. Dragonflies. F. F. Laidlaw, *Journ. Malayan Branch Roy. Asiat. Soc.* iv. 1926, pp. 214-233, figs. 1-5.
- vi. Dermaptera. A. Borelli, *t. c. s.* pp. 384-391, figs. 1, 2.
- vii. Fulgoroidea, Homoptera. F. Muir, *t. c. s.* pp. 392-412, figs. 1-34.
- viii. Homoptera - Fulgoroidea. C. F. Baker, *Philippine Journ. Sci.* xxxii. 1927, pp. 391-410, pl. i. text-figs. 1-13,....

The following are in the press :—

- Cicadidæ. J. C. Moulton.
- Membracidæ, Homoptera. F. Muir.
- Acrididæ (Orthoptera). C. Willemse.
- Pteridophyta. R. E. Holttum.
- Musci. H. N. Dixon.

The group is forested all over, and the collections were made at various localities near the Government stations of Siberut, in the island of that name, and Sioban in Sipora: they came from the sea-shore, low-lying ground, the swamps, cultivated areas, and from such hills as were accessible.

The islands are not very pleasant collecting-grounds: they are mostly swamp, out of which rise hills nowhere more than 1500 feet high and generally difficult to get at, being surrounded by soft ground. The sago-palm is common. The native villages are situated on the banks of rivers some distance upstream, and there are scarcely any paths except those made by the Dutch military posts: these are generally through flat land and are often untraversable owing to floods. There is much rain throughout the year. The islands are unhealthy: in spite of systematic employment of quinine and other precautions, all the members of a party of fifteen, except myself, suffered from malaria either on the islands or soon after leaving them.

As much on the latter account as because my period of absence from headquarters was limited, the Pagi Islands were not visited again. The lack of material from them, obtained in the same way and at much the same period as that from the other islands, has been a great handicap in working out the vertebrate collections. I do not think there is much left for the next visiting mammalogist to discover, but the systematist with adequate material available from the Pagi Islands and from the Batu Group to the north would probably distinguish further races. The present treatment of the collection is deliberately conservative.

The Mentawi Islands are apparently connected with each other by a sea-bottom of less than 100 fathoms, and most bathymographical charts show a connection with Sumatra, *via* the Batu Islands to the north-east, by a narrow ridge of similar soundings; but I am inclined to doubt whether this ridge is as unbroken as indicated, for the faunas of the groups differ greatly; while, though the Mentawi Islands possess a much richer mammalian fauna than the undoubtedly deep-water islands of Simalur and Engano at the extremities of the West Sumatran chain of islands, the fauna is much more peculiar and differentiated than that of Nias Island, also represented as being within the one-hundred-fathom line.

Apart from the connecting ridge, the group is surrounded by depths of 100–500 fathoms of water; further, everywhere directly between it and Sumatra lies the long Mentawi Basin with depths of 500–1000 fathoms. Such conditions render several of the West Sumatran Islands, in spite of small size and lack of height, quite as distinct from each other and from the rest of Malaysia as the larger areas of that sub-region are from each other.

Various hypotheses have been offered as to the former conditions of the West Sumatran Islands, but most of them were made by students of the reptilian faunas. Here we are dealing with the mammals, and the only deduction from them is that of Oldfield Thomas in 1895*, made at a time when the mammals of the islands and of Sumatra were so little known that it must be regarded as scarcely more than a venture.

Thomas considered that the Siporan mammals collected by Modigliani did not show the very slightest special relationship to Sumatra, and therefore that the West Sumatran Chain might be the remnant of a long peninsula or island, similar in shape to, but separate from, the Malay Peninsula or Sumatra. Such indications as these were suggested that the mammals, like other animals, showed a general similarity throughout the chain from the Nicobars to Christmas Island.

We do not yet know the faunas completely of course, but we know them fairly well; well enough—especially the mammals—to say to-day that but little similarity, except in the broadest sub-regional sense, exists between the mammals of the various island groups. Though some of these groups possess mammals subspecifically related to each other and to Sumatran forms, on the other hand the presence of several peculiar species not yet found, nor likely to be found, elsewhere is surprising; while very noticeable is the inequality of the various island faunas, some being rich, some extremely impoverished, some slightly differentiated, some very peculiar: yet they are mainly Sumatran.

A study of the faunas and of hydrographical charts now shows that during their mammalian history the various islands never

* Ann. Mus. Civ. Gen. (2a) xiv. 1895, p. 662.

all formed part of one vanished peninsula, never formed part of a vanished island, that they never were all connected with Sumatra at the same time, and that some of them perhaps were never connected with a main island or continent at all.

As a matter of fact, the West Sumatran Chain illustrates in a very interesting and clear manner the results of different environmental conditions: and in the following short discussion I have included the Andaman and Nicobar Islands, as their cases are parallel and they stand in much the same positions towards Indo-China as do certain West Sumatran Islands to the not very different subregion Malaysia.

There is given, to begin with, a hydrographic chart of parts of the western sides of Indo-China and Malaysia showing contour lines of 40, 100, and 500 fathoms, as these border the subregions between Burma and Java; and the positions of the various islands are shown within them.

To speak more precisely of the seas which separate the islands from the mainland and Sumatra:—

- Between Burma and Preparis Id. are depths of 33 fathoms.
- „ Preparis Id. and the Andamans occurs a sounding of 150 fathoms, and there may well be greater depths.
- „ the Andamans and Nicobars are depths of about 450 fathoms.
- „ the Nicobars and Sumatra are depths of about 800 fathoms.
- „ Sumatra and the Simalur Ids. are depths of more than 200 fathoms.
- „ Sumatra and the Banjak Ids. are depths of less than 35 fathoms.
- „ Sumatra and the Nias Id. are depths (*via* the Banjak Ids.) of less than 100 fathoms.
- „ Sumatra and the Mansalar Id. are depths of less than 20 fathoms.
- „ Sumatra and the Batu Ids. are depths of less than 25 fathoms*.
- „ Sumatra and the Mentawi Ids. are depths (*via* the Batu Ids.) of about 100 fathoms.
- „ Sumatra and the Engano Id. are depths of about 450 fathoms.

Or, to put it another way:—

Preparis Id.	in 33 fathoms	} are shallow-water islands inside the 40-fathom line.
Banjak Ids.	„ 35 „	
Mansalar Id.	„ 20 „	
Batu Ids.	„ 25 „	

* Excluding the unknown little islets of Simoek and Bodjo, which lie in deeper water.

Nias Id.	in - 100 fathoms	} are medium-water islands inside the 150-fathom line.
Mentawi Ids.	„ + 100 „	
Andaman Ids.	in + 150 fathoms	} are deep-water islands inside the 500-fathom line.
Nicobar Ids.	„ ± 450 „	
Simalm Ids.	„ + 200 „	
Engano Id.	„ ± 450 „	

(As nearly as they can be obtained from existing charts: but the soundings are inadequate where they are most needed; in particular to the north of the Andamans, between the Simalur Ids. and Sumatra, and between the Batu Group and the Mentawis.)

Taking the islands by groups, an analysis of their mammals* produces the table attached (pp. 802-805). I have endeavoured to trace the forms which have been described from them binomially or trinomially, with a local regard only, back to their original species in the interests of clarity and conciseness†. In most cases a group has been credited by mammalogists with a separate race on each island within it; in few cases has the same subspecies of terrestrial mammal been recognized from two or more islands in a group; and in scarcely any case is the same form, except among bats and commensal rats, recorded from two groups‡.

* *Vide* :—

Thomas, *tom. cit. supra*, pp. 660-672 (Sipora Id.).

Lyon, *Ann. & Mag. Nat. Hist.* (8) i. 1908, pp. 137-140 (Ratu Ids.).

Miller, *Proc. U.S. Nat. Mus.* xxiv. 1908, pp. 751-795 (Andaman and Nicobar Ids.).

Lyon, *Proc. U.S. Nat. Mus.* li. 1916, pp. 457-462 (a list of all the mammals obtained on the West Sumatran Islands between the years 1901-1905 by W. L. Abbott and C. Boden Kloss: with a bibliography).

Thomas, *Ann. & Mag. Nat. Hist.* (9) xii. 1923, pp. 591-593 (Simalur Id.).

† It should be said that my idea of a species is very comprehensive. Many mammalogists will not accept my treatment, for instance, of the *Paradoxures* of the Mentawi Group as subspecies of *P. hermaphroditus*, but would consider *P. lignicolor* to be a species with two subspecies. Nevertheless, however differentiated *lignicolor* and *sibiru* now are, it is still obvious that they are derived from, or are linked to, *P. hermaphroditus*, and are not of independent, unknown, or other origin.

The time for quadrinomials to express different degrees of relationship is not yet, or I would write of the West Sumatran Islands' palm-civets :—

Simalur Id. *P. hermaphroditus hermaphroditus parvus*.

Mentawi Ids. *P. hermaphroditus lignicolor lignicolor*.

P. hermaphroditus lignicolor sibiru.

Engano Id. *P. hermaphroditus hermaphroditus enganensis*.

‡ The rats of the Andamans and Nicobars are only tentatively referred to species, as so long a time has passed since I helped to collect them that I am uncertain of their affinities; but from Mr. G. S. Miller's descriptions (*loc. cit. supra*) the majority are races of *Rattus rattus*. A form of *Mus musculus* has been introduced into the Andamans.

MAMMALS OF THE ANDAMAN-ENGANO ISLANDS CHAIN (MICROCHIROPTERA excluded).

[Distribution of the species elsewhere:—I= Indo-Chinese Subregion (including Burma and Tenasserim).

M = Malay Peninsula. S = Sumatra. J = Java. B = Borneo.

ANDAMAN Ids. (deep water).	NICOBAR Ids. (deep water).	SIMALUR Ids. (deep water).	BANJAK Ids. (shallow water).	NIAS Id. (medium water).	MANSLAR Id. (shallow water).	BATU Ids. (shallow water).	MENIANG Ids. (medium water).	ENGANO Id. (deep water).
*	—	—	—	—	—	—	<i>Macaca nemestrina</i> , I.M.S.B.	—
—	<i>Macaca irus</i> , I.M.S.J.B.	<i>Macaca irus</i> .	<i>Macaca irus</i> .	<i>Macaca irus</i> .	<i>Macaca irus</i> .	<i>Macaca irus</i> .	—	—
—	*	—	—	—	—	<i>Presbytis femoralis</i> , I.M.S.B.	—	—
—	—	—	—	—	—	—	<i>Presbytis potenziani</i> .	—
—	—	—	—	—	—	—	<i>Simias concolor</i> .	—
—	—	—	—	—	—	—	<i>Hylobates klossi</i> .	—
<i>Paguma larvata</i> , I.M.S.B.	—	—	—	—	—	—	—	—
—	—	<i>Paradoxurus hermaphroditus</i> , I.M.S.J.B.	—	—	—	—	<i>Paradoxurus hermaphroditus</i> .	<i>Paradoxurus hermaphroditus</i> .
—	—	—	—	—	—	—	<i>Hemigalus derbyanus</i> , M.S.B.	—
—	—	—	—	—	—	<i>Arctogalidia trivirgata</i> , I.M.S.B.	—	—

[illegible]

* *Macaca nemestrina andamanensis*: introduced from Burma.

† Possibly present in a truly wild state.

† *Pittatus* section. '

MANUALS OF THE ANDAMAN-ENGANO ISLANDS CHAIN (MICROCHIROPTERA excluded)—continued.

[Distribution of the species elsewhere:—I=Indo-Chinese Subregion (including Burma and Tenasserim).

M=Malay Peninsula. S=Sumatra. J=Java. B=Borneo.]

ANDAMAN IDS. (deep water).	NICOBAR IDS. (deep water).	SIMALUR IDS. (deep water).	BAJAK IDS. (shallow water).	NIAS ID. (medium water).	MANGLAR ID. (shallow water).	BATU IDS. (shallow water).	MINTAWI IDS. (medium water).	ENGANO ID. (deep water).
—	—	—	—	—	—	<i>Lariscus</i> <i>insigne</i> , M.S.J.B.	—	—
—	—	—	—	—	—	—	<i>Lariscus</i> <i>siabo</i> , S.J.	—
—	—	—	<i>Ratufa</i> <i>bicolor</i> , I.M.S.J.	—	—	<i>Ratufa</i> <i>bicolor</i> .	—	—
—	—	—	<i>Ratufa</i> <i>affinis</i> , M.S.B.	—	<i>Ratufa</i> <i>affinis</i> .	<i>Ratufa</i> <i>affinis</i> .	—	—
—	—	—	<i>Sciurus</i> <i>tenuis</i> , M.S.B.	—	<i>Sciurus</i> <i>tenuis</i> .	<i>Sciurus</i> <i>tenuis</i> .	—	—
—	—	—	—	—	—	<i>Sciurus</i> <i>lowi</i> , M.S.B.	<i>Sciurus</i> <i>lowi</i> .	—
—	—	—	<i>Sciurus</i> <i>notatus</i> §, M.S.J.B.	—	<i>Sciurus</i> <i>notatus</i> §.	<i>Sciurus</i>	—	—
—	—	—	—	—	—	<i>Sciurus</i> <i>notatus</i> §.	<i>Sciurus</i> <i>melanogaster</i> .	—
<i>Rattus</i> <i>rattus</i> . I.M.S.J.B.	<i>Rattus</i> <i>rattus</i> .	<i>Rattus</i> <i>rattus</i> .	—	<i>Rattus</i> <i>rattus</i> .	—	—	<i>Rattus</i> <i>rattus</i> .	<i>Rattus</i> <i>rattus</i> .
—	—	<i>Rattus</i> <i>concolor</i> , I.M.S.J.B.	—	<i>Rattus</i> <i>concolor</i> .	—	—	—	—
—	—	—	—	—	—	—	—	—
<i>Rattus</i> <i>muelleri</i> ? M.S.B.	<i>Rattus</i> <i>muelleri</i> ?	—	<i>Rattus</i> <i>muelleri</i> .	—	<i>Rattus</i> <i>muelleri</i> .	<i>Rattus</i> <i>muelleri</i> .	—	<i>Rattus</i> <i>enganus</i> .
—	—	—	<i>Rattus</i> <i>whiteheadi</i> , M.S.B.	<i>Rattus</i> <i>whiteheadi</i> .	—	<i>Rattus</i> <i>whiteheadi</i> .	—	—

Omitted from the table are Preparis Id. in the north and Christmas Id. in the south. The first is in shallow water: its mammals have not been sufficiently investigated, but a crab-eating Macaque (*M. irus*) and a *Sciurus* occur. The last is an oceanic island surrounded by seas of over 5000 fathoms: rats, a musk-shrew, and bats are its only mammals.

Scrutiny of the table shows how variable is the mammal fauna of the Andaman-Engano Chain, and frequently how little in common have two adjacent groups. The mammal faunas of the deep-water islands—Andamans, Nicobars, Simalurs, Engano—are extraordinarily poor, and consist largely of units that may have been introduced—such as the Macaques, the palm-civets, the pigs, the musk-shrews, and some of the rats: even the Nicobar *Tupaia* is difficult to account for in any other manner, though now a very distinct animal. The Nicobars are the only deep-water islands known on which Tupaiidæ occur: sea-depths of 800 fathoms separate them from Sumatra, while had *T. g. nicobarica* arrived from the north over what is now a 450-fathom strait we ought to find the genus in the Andamans. Conditions in the latter suggest that they are more deeply separated from Burma than the few soundings indicate. All the above islands, relevant to their present faunas, may never have been connected with Burma or Sumatra at all.

The shallow-water coastal islands—the Banjaks, Mansalar, and the Batu Ids.—are essentially normal save that the first possesses, as far as is yet known, the unique murine genus *Lenothrix*; while hitherto the only small island on which *Ptilocercus* has been found, except Pulau Pinie in the Batu group, is Great Karimon Id. on the east coast of Sumatra (where it also occurs on the larger Banka Id.).

It is when we consider the medium-water islands that interesting comparisons arise. The fauna of Nias is rather poor, but normal for its surroundings: it is a somewhat accidental and modified fauna owing to the sea-depths in which the island stands, and appears to have been derived from Sumatra via a bridge that included the Banjak Ids., though several terrestrial species occur that have not been taken in the latter (and *vice versa*): all, however, are present in Sumatra. It has races of Megachiroptera that have not been met with anywhere else.

The Mentawi Group is in several respects truly abnormal. It has a distinct genus of langur (*Simias*) not known elsewhere; distinct species of gibbon and langur that cannot be referred to others; a form of *Macaca nemestrina*, a species not usually found on small islands; remarkably distinct subspecies of *Paradoxurus hermaphroditus*; a representative of *Hemigale derbyanus*, another animal not known from small islands; a local race of *Cervus unicolor*; three members of "*Sciuropterus*" allied to Sumatran animals, but a genus (*s. g.*) not known in any form from the rest of the chain; a race of *Lariscus niobe*; an endemic squirrel (*Sciurus melanogaster*) and *Manis javanica*. None of these have been found in the Batu Islands which represent any

bridge that may have led from Sumatra. In common with the former and with Sumatra are *Tupaia glis*, *Sciurus lowi*, *Rattus surifer*, and *Rattus sabanus*.

On the other hand, the group has no crab-eating Macaque, generally so ubiquitous; no Muntjak or *Tragulus*; no wild pigs (?); no *Petaurista*; no representative of *Ratufa* or *Sciurus notatus*, *Sciurus tenuis*, or *Crocidura* or *Porcupine*, or of several other Sumatran species found in the Batu Ids. (*q. v.*). So though we can trace the derivation of part of its fauna from Sumatra, there are many anomalies that we cannot explain.

Of the volant mammals of the chain, we can only regard the fruit-bats, or Megachiroptera, as at all well known. Of these, one group (or species as I prefer to call it), *Pteropus melanotus*, is confined, though unevenly distributed, to the chain under discussion, including Christmas Island (one medium-water, three deep-water, one oceanic island). In Malaysia the presence of *Pteropus vampyrus* on such islands as Nias and Siberut is unusual, though it inhabits the North Natuna Group: its occurrence in the Andamans and Nicobars is very doubtful. In islands of these kinds it is generally replaced by *P. hypomelanus*, which is not found on the continent or on any of the large land-masses. Nias has evolved two well-marked forms of *Cynopterus* conspicuous for their large size, not yet met with anywhere else, but related to Sumatran animals.

To sum up:—The shallow-water islands are quite normal for their situation, for *Lenothrix*, known from one example only, is so rare, or of such a habit, that it may well occur elsewhere and have been missed. The impoverished terrestrial mammal fauna of the deep-water islands, to which the Andaman Group may later actually prove to belong hydrographically (as it does faunistically), is also normal: even of the few mammals they possess, some may have arrived fortuitously. Of the medium-water islands, Nias is fairly normal, *Arctictis* being perhaps the only unexpected terrestrial species, with *Manis* (also occurring in the Mentawi Group). All have derived their land mammals from the adjacent continental areas—Indo-China and Malaysia. The Mentawi Islands are abnormal: they are continental, and in part their mammals are related to those of Sumatra; but there are some which are subspecifically extremely distinct, and yet others which appear to be strictly endemic. The only outstanding feature of all the islands as a whole is the presence of the *Pteropus melanotus* bats, which are confined to the Andaman-Christmas Island Chain. This single common factor will not support the postulation of a bygone continuous land-area, of which this long chain of islands is a relic.

The Andaman-Christmas Island Chain does not form an independent subregion, but is part of Indo-China and Malaysia, which (when their borders lie in the sea) are everywhere bounded by a contour-line of 100 fathoms. Some of these islands, which lie in greater depths and not upon the Sunda Shelf, and these only, are naturally somewhat aberrant.

II. SYSTEMATIC.

1. *Hylobates klossi*.
2. *Pithecius potenziani potenziani*.
3. *Pithecius potenziani siberu*, subsp. n.
4. *Simias concolor concolor*.
5. *Simias concolor siberu*, subsp. n.
6. *Paradoxurus hermaphroditus lignicolor*.
7. *Paradoxurus hermaphroditus siberu*, subsp. n.
8. *Hemigalea derbyana sipora*, subsp. n.
9. *Cervus unicolor oceanus*, subsp. n.
10. *Petinomys lugens*.
11. *Iomys horsfieldi sipora*, subsp. n.
12. *Hylopates aurantiacus*.
13. *Sciurus melanogaster melanogaster*.
14. *Sciurus melanogaster mentawi*, subsp. n.
15. *Sciurus lowii fruterculus*.
16. *Sciurus lowii siberu*, subsp. n.
17. *Lariscus niobe obscurus*.
18. *Lariscus niobe siberu*, subsp. n.
19. *Rattus sabanus siporanus*.
20. *Rattus surifer pagensis*.
21. *Rattus rattus mentawi*, subsp. n.
22. *Rattus rattus diardi*.
23. *Tupaia glis chrysogaster*.
24. *Tupaia glis siberu*, subsp. n.
25. *Pteropus hypomelanus euganus*.
26. *Pteropus vampyrus malaccensis*.
27. *Cynopterus angulatus*.
28. *Macroglossus minimus fraternus*, subsp. n.
29. *Emballonura monticola*.
30. *Myotis muricola*.
31. *Kerivoula hardwickii engana*.

III. ACCOUNT OF THE COLLECTION.

1. *HYLOBATES KLOSSI* (Miller).

Symphalangus klossii Miller, Smith. Misc. Coll. xlv. 1903, p. 70, pls. xvii.-xix. : South Pagi Island.

Sipora : 1 ♂, 1 ♀.

Siberut : 6 ♂, 2 ♀.

On the general configuration of the skull this gibbon could be referred to either *Hylobates* or *Symphalangus*. It resembles the latter in that the mandibular symphysis is rather more vertical than in the typical gibbons, but in the rounded form of the occipital region its affinities are with *Hylobates*.

The skull is relatively narrower, especially in the mastoid region, than in other gibbons.

As in the members of both genera, the second and third toes are partially united, but not to the same extent as in *Symphalangus*, and only slightly more so than in some examples of *Hylobates mülleri*, *gabrielli*, and *lar*. The general character of the pelage seems to agree with the gibbons: but they vary considerably in this respect; and this is no doubt a character, like colour, to which too much importance must not be attached. In most of the typical gibbons we have examined the hair on the outer side of the forearm points towards the wrist: in the siamang it points to the elbow.

Among the Mentawi animals the two Sipora specimens have the hair pointing towards the elbow as in our siamangs, but in the Siberut series the hair on the distal half of the outer forearm points towards the wrist.

A mounted topotype from the Pagi Islands has the hair of one forearm pointing towards the wrist and of the other towards the elbow.

None of the Malaysian *Hylobates* is entirely black, but a parallel case to *klossi* is provided by *hainanus* of Hainan.

The well-clothed throat and the characteristic gibbon "song" in both sexes of *klossi* are the chief reasons why we place it in the genus *Hylobates* *.

Elliot's statement (Rev. Prim. iii. 1912, p. 180) that *klossi* "is a very small form of the siamang, differing from it in no respect save in size" is as incorrect as his statement on p. 176 (*t. c. s.*) that this species possesses a laryngeal sac.

The difference in the digital webbing in *Symphalangus* and *Hylobates* (in which latter genus it is subject to a great deal of individual variation) is one of degree only.

The differences in the direction of the hair on the forearm are bridged by the Mentawi animals. The jaw of *klossi* is also intermediate, the profile of the chin and ascending ramus being less vertical than in the siamang, but more so than in the gibbons.

There is nothing in these characters on which generic differences can be based, and there remain therefore only, in the siamang, greater size, the bare throat, and the laryngeal sac which produces the different voice. These also do not seem to us to be of more than marked specific value. We feel therefore that there are insufficient grounds for treating the siamang as the type of a distinct genus; but had our opinion been otherwise we should have placed the Mentawi animals in *Hylobates* and not in *Symphalangus*.

(For measurements see p. 810.)

* Dr. W. L. Abbott's schooner 'Terrapin' anchored off the Pagi Islands one afternoon in 1902; and I well remember the astonishment with which we heard at sunrise next day the undoubted cries of gibbons from the forest of these small islands. Nobody who has heard the voice of both gibbon and siamang can possibly mistake the two.—C. B. K.

TABLE OF MEASUREMENTS (in millimetres).—Measurements of hind feet are always exclusive of claws.
Hylobates klossi (p. 808).

Locality.	Sex.	Head and Body.	Hind foot.	Skull.				Collector's No.	Remarks.
				Greatest length.	Basal length.	Zygomatic breadth.	Maxillary tooth-row with canine (alveoli).		
Sipora	♂	435	126	100	72.6	69	30	2230	Adult.
"	♀	430	126	99.5	69.6	63.8	31	2364	"
Siberut	♂	450	135	103.8	72.1	68	30	2043	"
"	♂	435	137	101.3	69.7	70	29	2054	Subadult.
"	♀	433	126	97.4	67	67	28	2044	Adult.
"	♀	433	133	100.1	69.8	65.3	27.7	2094	"

2. *PITHECUS POTENZIANI POTENZIANI* (Bonap.) *.

Semnopithecus potenziani Bonap. Comptes Rendus, xliii. (1856) p. 412, note; Thos. 1895, p. 663.

Sipora: 3 ♂, 2 ♀.

We select Sipora Island as the type-locality of this monkey, which we must regard as a species since we cannot ally it with anything previously described.

Blyth, with coloured drawings of the co-types before him, said that the young was wholly pale ferruginous: Blanford, who saw the specimen, records it as wholly rufous-white or pale isabelline: Elliot describes it as yellow.

A juvenile animal taken from the breast on Sipora Island is, it is interesting to note, far more like the Siberut form than its own parents. It differs from *P. p. siberu* in having a little grey-white on the crown and hind limbs, the lower side of the tail greyish-white for two-thirds the length basally, rufous on the shoulders, and in being less blackened on the lower side of the trunk. It would seem therefore that *P. p. siberu* is the more primitive form.

Two faded mounted specimens from the Pagi Islands (1902) do not appear separable.

Blanford (Faun. Brit. India Mamm. 1888, p. 38) and Elliot (Rev. Prim. iii. 1912, p. 67) both say that Bonaparte's description is insufficient, though the latter uses Bonaparte's name for this monkey. Thomas (1895) considered the name valid. We have not seen Bonaparte's reference, but if it is inadequate, the next name available seems to be *Presbytes chrysogaster*. Blyth in 1875 (Journ. Asiat. Soc. Bengal, xlv. part ii, extra number, p. 10) issued a description under this name from coloured drawings supplied by Peters which were subsequently published in 1879.

"Face black, lips dusky-fleshy."

(For measurements see p. 812.)

3. *PITHECUS POTENZIANI SIBERU*, subsp. n. (Pl. I.)

Type—Adult male (skin and skull), collected on Siberut Island, West Sumatra, on 13th September, 1924. Raffles Museum, No. 2005.

Characters.—Like *Pithecus potenziani potenziani*, but with the rufous underparts of that form replaced by black or dull brown.

* It is difficult to know what generic name to use for these monkeys. In 1895 Thomas selected *Simia vester* for the type of *Pithecus*, and, as it was even generically indeterminate, consigned *Pithecus* to the "limbo of unrecognisable names."

In 1915, Lyon regarded this action as final under the International Code of Zoological Nomenclature, and to support the validity of Thomas's action re-selected *vester* as the type of *Pithecus*.

In 1916, Thomas reversed his opinion and revived *Pithecus* because he felt able then to determine generically *S. teter* as some sort of langur or other.

The first generic name for the langurs and lotongs about which there is no possible doubt whatever is *Pygathrix* (E. Geoffroy, 1812; type *S. nemus* Linn.).

Pithecius potenziani potenziani (p. 811). *P. potenziani siberu* (p. 811).

Species and Locality.	Sex.	Head and body.	Tail.	Hind foot.	Head to symph. pubes.	Skull.				Collector's No.	Remarks.
						Greatest length.	Basal length.	Zygomatic breadth.	Maxillary tooth-row with canine (alveoli).		
<i>Pithecius P. potenziani.</i>											
Sipora	♂	505	590	180	—	97.4	70.9	77.2	33	2313	Adult.
"	♂	495	595	180	545	100.3	71.9	77	33.5	2389	Subadult.
"	♂	540	610	162	—	—	—	81.4	33(±)	2349	Adult.
"	♀	510	605	152	—	88.5	64	70	31.3	2314	Subadult.
"	♀	485	640	156	550	95	69	75	33	2365	"
<i>P. P. siberu.</i>											
Siberut	♂	500	580	155	550	93	65	74	31	2005	Adult: Type.
"	♂	435	495	148	490	89.2	62.9	—	33	2024	Adult.
"	♂	485	550	150	550	99.5	68.4	74	32.3	2085	"
"	♀	465	545	150	517	89	59	66.3	—	2025	Immature.
"	♀	390	450	130	435	87.4	56.3	61.2	—	2159	"

Colour.—Upper parts, limbs, and tail glossy black. On the neck, shoulders, and mantle the hairs have the basal two-thirds grizzled with ochraceous-buff, but this is rarely apparent unless the pelage is disturbed. Forehead (narrowly), sides of the face, and throat white, tipped with black on the throat. Underparts between tawny and ochraceous-tawny (type), but all the hairs strongly tipped with black, which gives the appearance of a blackish wash. A median area on the chest darkest, being frequently broadly black. A white pubic patch.

"Face black, fading to dusky fleshy round the mouth."

Skull and teeth.—Very like *P. p. potenziani*, but the zygomatic breadth less; the two series are, however, badly matched as regards age.

Measurements.—See p. 812.

Specimens examined.—The type and four others, all from Siberut.

Remarks.—This is a good but variable form, separable at sight from *p. potenziani* by reason of its blackened underparts. There is never any approach to the bright colouring of *P. p. potenziani*. While the colour of the abdomen of the more brightly coloured examples of *siberu* is tawny, the dullest Siporan animals are ferruginous below.

4. *SIMIAS CONCOLOR CONCOLOR* Miller.

Simias concolor Miller, Smith. Misc. Coll. xlv. 1903, p. 67, pls. xiv.-xvi. South Pagi Island.

Sipora: 1 ♂, 3 ♀.

We have little to add to Miller's very complete description of this remarkable monkey.

The above specimens seem similar to our topotypes of *concolor* when allowance is made for a small amount of fading in the latter, which were collected in 1902.

The darkening of the hands and feet, as mentioned in the original description, is almost imperceptible in all but the male, in which the feet are conspicuously darker than the deep brown of the hind limb. A profile sketch of the face made by Kloss from a specimen in the flesh does not differ materially from his photograph published by Miller (*loc. cit.*), but the nose is perhaps slightly more prominent and retroussé.

"Face, hands, tail, and callosities black."

(For measurements see p. 814.)

5. *SIMIAS CONCOLOR SIBERU*, subsp. n. (Pl. II.)

Type.—Adult male (skin and skull), collected on Siberut Island, West Sumatra, on 25th September, 1924. Raffles Museum, No. 2085.

Diagnosis.—Like *S. concolor* from Sipora Island, but darker,

PROC. Zool. Soc.—1927, No. LIV.

Simias concolor concolor (p. 813). *S. concolor siberu* (p. 813).

Species and Locality.	Sex.	Head and Body.	Tail.	Hind foot.	Head to symph. pubes.	Skull				Collector's No.	Remarks.
						Greatest length.	Basal length.	Zygomatic breadth.	Maxillary tooth-row with canine (alveoli).		
<i>Simias c. concolor</i> .											
Sipora	♂	490	130	165	540	104	74.1	82.5(±)	36.	2411	Aged.
"	♀	480	130	155	505	95.8	66.4	66	30.8	2410	Subadult.
"	♀	478	152	105	530	99.1	70.2	70	32	2409	"
"	♀	420	130	155	465	89	61.3	61.9	—	2357	Immature.
<i>S. c. siberu</i> .											
Siberut	♂	515	155	160	565	96	65.9	72.5	32.5	2085	Adult: Type.
"	♀	465	120	150	—	96.5	65	72.3	31.2	2011	Subadult (var.).
"	♀	480	150	148	515	95.2	66	71	31.2	2086	Adult.

especially on the rump. The limbs almost concolorous with the black hands and feet, and much darker than clove-brown. Underparts fuscous-black and very distinct from the paler underparts of *c. concolor*.

Measurements.—See p. 814.

Specimens examined.—One male (type) and two females, all from Siberut.

Remarks.—Although we cannot separate our single normal female from Siberut from three obtained in Sipora, the characters presented by the type, an adult male, could scarcely be within the range of individual variation, and we feel sure that here is another case of a species with its darkest race in the northern island.

The skulls of the Siberut females though shorter are actually broader than those of the Siporan females: at the same time they are somewhat older. No comparison is possible between male skulls, as the Siberut animal is much less aged than the other.

No. 2011, a female, is a handsome cream-coloured aberration. The whole of the upper parts and outer side of the limbs are cream-buff, washed on the nape, shoulders, and mantle with rich tawny, which latter colour is continued narrowly half-way down the median line. Underparts between cream-buff and ivory-yellow, very slightly brownish on the flanks and abdomen. Fore-arm, hands, and feet almost white, the blackened skin clearly visible through the hair. Face black, tail greyish-black, nails white.

It may be noted that the type series of *Simias concolor* contained two cream-buff varieties from small islands off South Pagi.

6. PARADOXURUS HERMAPHRODITUS LIGNICOLOR Miller.

Paradoxurus lignicolor Miller, Smiths. Misc. Coll. xlv. 1903, p. 44, pls. iv., v. North Pagi Island.

Sipora: 1 ♂, 1 ♀ ad.; 1 ♂, 8 ♀ juv.

On description these specimens appear to be *lignicolor*: both the adults have the tail rather lighter than the body, but in the young animals this is not so. The skull and teeth differ from those of *h. hermaphroditus* in precisely the characters given by Miller for *lignicolor*—viz., the interpterygoid space is narrower, the nasals are flat posteriorly, the teeth are larger, and the inner lobe of the upper sectorial is longer, the width of the palate being reduced.

In one adult (No. 2367) a median dorsal line is faintly visible, and in certain lights it is possible to trace the lateral stripes and spots of *hermaphroditus* in both the immature skins. *P. lignicolor* appears to be only a well-marked subspecies of *hermaphroditus*, but its likeness to *P. aureus* Cuv. of Ceylon should not be overlooked. In that island *P. aureus* seems to have the same

Paraloxerus hermaphroditus lignicolor (p. 815). *P. hermaphroditus siberu* (p. 817).
Hemigalea derbyana sipora (p. 817).

Species and Locality.	Sex.	Head and body.	Tail.	Hind foot.	Ear.	Skull.						Collector's No.	Remarks.	
						Greatest length.	Basal length.	Condylar-basal length.	Palatal length.	Breadth of palate between sectoria.	Least breadth of interpterygoid space.			Zygomatic breadth.
<i>Paradoxurus hermaphroditus tignicolor.</i>														
Sipora	♂	480	340	72	34	106.5	95	99.8	47.6	14	6.8	61.4	39.4	2366 Adult.
"	♀	450	380	71	33	103.5	94.3	99.5	47	14.1	7	57	38.9	2367 "
"	♂	360	315	65	32	—	—	—	—	—	—	—	—	2326 Juvenile.
"	♀	377	335	62	34	—	—	—	—	—	—	—	—	2195 "
<i>P. h. siberu.</i>														
Siberut	♂	375	325	69	34	90.5	80.6	85.2	42	12.9	6	44.5	—	2090 Juv.: Type.
<i>Hemigalea derbyana sipora.</i>														
Sipora	♂	490	295	79	34	100.2	91.3	96.5	50.7	14.8	4.2	52	38.2	2390 Ad.: "

distribution as *P. h. typus**, and therefore is probably a species distinct from it.

The tails of the Mentawi animals are shorter in proportion to the body-length than those of the typical *Paradoxurus*. Phillips ('*Spolia Zeylonica*,' xiii. 1925, p. 161) says the same of *aureus*. (For measurements see p. 816.)

7. *PARADOXURUS HERMAPHRODITUS SIBERU*, subsp. n.

Type.—Juvenile male (skin and skull), collected on Siberut Island, West Sumatra, on 25th September, 1924. Raffles Museum, No. 2090.

Characters.—Like *lignicolor* of Sipora Island, but noticeably lighter on the upper surface, and the tail very conspicuously lighter than the body. *P. lignicolor* from the Pagi Islands has the tail lighter than the body ("belly and tail buffy throughout"). In the present form the tail is very different from any other part of the body.

Colour.—Tawny-olive above, lighter in tone than *lignicolor* (Sipora). No darkened median line and no trace of spots. Underparts and inner surface of the limbs buffy. The tail much lighter than the rest of the body and between cinnamon-buff and clay-yellow.

Skull and teeth.—Compared with the Sipora series the bullæ are proportionately markedly larger.

Measurements.—See p. 816. Dentition: dm. 1-4.

Specimens examined.—One, the type.

Remarks.—Were it not for the fact that we have for comparison two juvenile examples of the Sipora animal, which, judging by their external measurements and cranial characters, are almost identical in age with the Siberut specimen we have made the type of this new form, we should scarcely have ventured to describe it as new. As it is, the differences are too strong to be ignored.

8. *HEMIGALEA DERBYANA SIPORA*, subsp. n.

Type.—Adult male (skin and skull), collected on Sipora Island, West Sumatra, on 1st November, 1924. Raffles Museum, No. 2390.

Characters.—About the size of *H. hardwickii* or perhaps a little smaller, but greyer and darker with marked cranial differences. Differs from *H. minor* Miller, of the Pagi Islands (Smiths. Misc. Coll. xlv. 1903, p. 43, pl. iii.), in having the dorsal bands not wider than in *hardwickii* and the nuchal stripes well defined.

Colour.—Upper surface and the sides of the limbs buffy-grey, the very pale buff tips to the hairs producing a frosted appearance. Dorsal markings black, well defined, and exactly as in *hardwickii* except that the stripes on the head are a little less

* *Viverra niger* Desm. (1920) is preoccupied by *Viverra niger* Peale & Beauvais (1796). *Paradoxurus typus* Cuv. (1821: Pondicherry) is the succeeding name.

distinct (not because they spread, but because they are on a darker ground). Underparts brownish-buff, the hairs all tipped with whitish-buff. Tail black except for two basal rings and the proximal half of the under surface, which are greyish-buffy.

Skull and teeth.—In size similar to some examples of *hardwickii*, but differing in practically the characters noted by Miller (*l. c. s.*) for *minor*. Audital bullæ smaller and less dilated; interpterygoid space narrower and longer; the postorbital constriction greater and much better defined. It may also be added that the palate is narrower. There appears, however, to be little if any difference in the size of the teeth.

Measurements.—See p. 816.

Specimens examined.—One, the type.

9. *CERVUS UNICOLOR OCEANUS*, subsp. n.

Type.—Two antlers, with frontal bones and other parts of the cranium attached, obtained on Siberut Island, West Sumatra, in September 1924. Raffles Museum, No. 2427.

Diagnosis.—A race of *C. unicolor* characterised by small size.

Measurements of type.—Circumference of antler above burr 140 (143)*; length of antler along convexity of curve 333 (310); burr to tip of brow-tine along convexity 215 (83); tip of apical tine to its angle with main trunk of antler 107 (80); median circumference of pedicel 106 (102); internal height of pedicel 16 (17); median frontal suture 97 (86).

Specimens examined.—The type and a fawn (skin and skull) from Siberut and one pair of antlers from Sipora (October 1924).

Remarks.—The Siberut antlers are older and more worn than those from Sipora, from which the velvet has only recently been lost. We have compared them with a number of Malayan examples in both conditions and of approximately equal size, and we find that the pedicels of the Mentawi animals are much shorter and stouter.

Examination of a series of some seventy Malayan heads shows that lighter horns and long slender pedicels belong to young animals, adult and aged animals having heavy horns and short stout pedicels.

It is reasonable to conclude, therefore, that the Mentawi specimens are full-grown animals representing a small race: furthermore, the frontal bones are shorter, often much shorter, than in young Malayan stags. *Cervus unicolor brooki* Hose, of Borneo, has also a long frontal and long slender pedicels when young. *C. kuhli* M. & S., from Bawean Island, Sava Sea, is a small animal, but has notably long pedicels.

The fawn is of the usual foxy-red colour with a broad dark stripe down the spine.

* Measurements are in millimetres; those in parentheses are of a second pair of antlers from Sipora.

10. PETINOMYS LUGENS (Thomas).

Sciuropterus lugens Thos. 1895, p. 666: Sipora.

Sipora: 7 ♂, 13 ♀.

We have little to add to Thomas's description of this flying squirrel beyond noting that of our series it would not be accurate to say "of a uniformly dark colour above and below." The underparts are very scantily clothed, but the hair itself is mostly of a brownish-smoky colour, brownest on the throat. In some specimens the distal portion of the hairs are brown, but even in these the underparts are never so dark as the upper parts, and are best described as smoky- or dark slaty-grey.

Examples in fresh pelage are very dark above (brownish-black) with only a faint tinge of brown. Those in worn condition are quite brown in places, this being particularly noticeable in "bleached" examples at the root of the tail.

Three specimens show a short, faint, white streak on the middle line of the breast; in one there is a conspicuous white patch about half an inch broad, and in yet one other there is a large white patch of about 100 by 50 mm. The others are immaculate below. The juvenile is exactly like the adults. There are three pairs of inguinal mammae. This squirrel probably represents a smallish local form of *P. hayens* (Jent.), from Deli, N.E. Sumatra, but we have not seen this last example.

(For measurements see p. 820.)

11. IOMYS HORSFIELDI SIPORA, subsp. n.

Type.—Adult male (skin and skull), collected on Sipora Island, West Sumatra, on 13th October, 1924. Raffles Museum, No. 2243.

Characters.—About the size of *I. h. davisoni*, but on account of its very dark coloration not requiring close comparison with any other known member of the genus. External structural characters as in *davisoni*, but the tail scarcely distichous.

Colour.—Cheeks, upper surface, and tail brownish-black, the base of the pelage slaty. The outer sides of the limbs and body and the membranes grizzled with buff. Underparts light slaty-grey, the hairs of all parts except the throat being tipped white or very pale buff, producing a silvered or frosted appearance.

Skull.—Longer and relatively narrower than that of *davisoni*, and owing to the much less inflated condition of the mastoid region, the posterior portion of the cranium is actually much less broad and square.

Measurements.—See p. 820.

Specimens examined.—The type and one other from Sipora.

Remarks.—This squirrel bears a most striking superficial resemblance to *Petinomys lugens*, but close comparison of the two species reveals many differences. *I. h. sipora* has larger, broader ears which also lack the marked concavity on the outer margin; it is without the long hairs on the cheeks and aural region and the feet are much less robust.

The second example obtained is an immature female. It differs from the type in having the whole of the flanks, thighs, and the upper surface of the parachute grizzled.

12. HYLOPETES AURANTIACUS (Wagl.).

Sciuropterus aurantiacus? Thos. 1895, p. 668.

Sipora: 1 ♀.

We follow Thomas in referring this small flying squirrel of Sipora to *aurantiacus* (Wagl.) of Banka. In dimensions it also agrees with *Sciuropterus amoenus* Miller (Proc. U.S. Nat. Mus. xxxi. 1906, p. 264: Kundur Id., Rho Archipelago).

The single immature specimen obtained has the skull damaged, and the measurements of length are not precise.

Collector's external measurements—Total length 300; head and body 140; tail 160; hind foot 30; ear 17.

Cranial measurements.—Greatest length 37; condylo-basilar length 32.5; basilar length 29.4; palatilar length 16.7; diastema 9.2; nasals 9.9 × 5; interorbital breadth 8.2; maxillary tooth-row (alveoli) 7.2.

Colour.—Upper parts ochraceous-tawny, but the hairs so sparsely tipped that the dark slate bases show through practically everywhere. Feet dark. Underparts buff, the dark bases of the hairs on the undersides of the limbs and abdomen showing through and causing these parts to be tinged with grey. Cheeks, throat, chest, and mesial line orange-buff; a small white patch on the chest. Tail non-distichous, dull black, tipped with white and washed with smoky-brown at the base.

While we have little doubt that this specimen belongs to a distinct race, it is subadult and represents a form which should exhibit a pelage somewhat brighter above.

13. SCIURUS MELANOGASTER MELANOGASTER Thomas (Pl. III. fig. 1.)

S. melanogaster Thomas, 1895, p. 668: Sipora Island.

Sipora: 20 ♂, 16 ♀.

Like that to be described next, this squirrel is so very unstable that the description of any one example would scarcely suffice to represent the form. Seen from above, some specimens are much colder in tone than others, and some again almost show a tendency to rufous on the outside of the thighs. Blackening takes place chiefly on the head. Some, as mentioned by Thomas, have the cheeks and ears nearly, or quite black; but in others these parts are scarcely dusky.

The tail may be grizzled exactly like the back, or almost black with the grizzling much reduced. In only a few instances can it be definitely said that there is no reddish "pencil." The underparts are always black; but there is a considerable amount of variation in the colour, which may be more or less intense or

merely smoky, and in the amount of frosting due to the intermingling of white hairs.

A point of considerable importance is that in most of the specimens of the large series before us a double pair of lateral stripes seem present, although they can be easily overlooked. The buff stripe is indicated by a more coarsely grizzled area and the black stripe by an intensification of the colour of the underparts.

This is a medium-sized animal, quite unlike any other Oriental species, but we are inclined to regard all the large Mentawi squirrels as forms of *nigrovittatus*, although they are rather large. This is admittedly an extreme view to adopt, and the new form described below from Siberut is, by itself, scarcely recognisable as belonging to the group—tawny-bellied individuals being suggestive rather of *notatus* from East Java.

S. atratus Miller, from the Pagi Islands, has the two lateral stripes much reduced, and the black one in some cases shows a tendency to spread over the grey belly. In *melanogaster* the whole of the underparts is usually black, but the pale stripe is still noticeable; in *mentawi* the underparts are largely rufous, the pale stripe is still present, but the dark one is only to be noted as a slightly richer part of the rufous area.

(For measurements see p. 823.)

14. *SCIURUS MELANOGASTER MENTAWI*, subsp. n. (Pl. III. fig. 2.)

Type.—Adult male (skin and skull), collected on Siberut Island, West Sumatra, on 16th September, 1924. Raffles Museum, No. 2026.

Characters.—Nearest to *melanogaster* Thos., of Sipora Island, from which it differs in having the underparts wholly or in part reddish-brown instead of black.

Colour.—Above grizzled black and ochraceous-buff, lighter on the fore limbs and darkest on the tail, where the black predominates. The thighs more warmly coloured than the rest of the upper parts and almost imperceptibly washed with rufous. The head and cheeks dullest (more buffy-grey). Feet buffy. Underparts light reddish-brown. On the flanks an indistinct buffish stripe from axilla to thigh, beneath which a slight darkening of the reddish-brown underparts possibly indicates a second lateral stripe.

Skull.—Essentially as in *S. m. melanogaster*.

Measurements.—See p. 823.

Specimens examined.—Seventeen males and twenty-seven females from Siberut Island.

Remarks.—The large series before us agrees with the type in having the tail noticeably darker than the rest of the upper parts. A rufescent pencil is evident in the majority. The feet may be light or dark. On the underparts the forty-four specimens are roughly divisible into three series. Thirteen agree with the type in being completely reddish-brown; fourteen have

Sciurus melanogaster melanogaster (p. 821). *S. melanogaster mentawi* (p. 822).

Species and Locality.	Skull.												Collector's No.	Remarks.
	Head and body.	Tail.	Hind foot.	Ear.	Greatest length.	(Condylar-basal length.	Palatilar length.	Diastema.	Upper molar row.	Median nasal length.	Interorbital breadth.	Zygomatic breadth.		
<i>Sciurus melanogaster melanogaster.</i>														
Nipona	205	170	46	17	51	43.7	21.6	11.5	10.2	16	16.5	30.5	2184	Adult.
"	204	172	49	17.5	51.7	44	22.5	12.5	10.2	15.5	16.5	30	2185	"
"	215	165	46	17	52	44.9	23	12.5	10	17	17	30.6	2206	"
"	206	177	50	17	52	44.8	22.7	11.8	10	16	16	30	2206	"
"	207	175	48	17	52.1	44.8	23	13	10	17	—	30.1	2214	"
"	218	190	47	17	52.3	45.6	22	12	10.6	15.5	17	30.5	2206	"
"	208	177	50	17	52	44.1	22.9	11.8	10.8	16.1	17.5	30.1	2207	"
"	210	190	50	16.5	53.9	46	23	12.3	10.4	16	16.8	31	2235	"
"	218	193	45	18	54	45.1	23	12.4	10.9	18	16.9	30.5	2293	"
"	215	165	45	17	52.5	44.8	22.9	12.4	10.3	16.6	18	31.9	2309	"
<i>S. m. mentawi.</i>														
Siberut	215	175	48	17	51.3	46.8	24	12.9	10.2	18.5	17.8	32	2626	Adult: Type.
"	210	180	47	17	52.3	45.2	22.9	12.4	9.9	17.1	17	31	2011	"
"	210	170	47	18	52.5	45.5	23.5	13	10	18	16	30	2057	"
"	214	180	48	17	52.5	45.2	23	12.8	10.3	17	16	30	2060	"
"	210	180	48	18	52.7	45.2	23.5	13	10	17.1	16.2	30	2080	"
"	224	166	47	19	52.5	45	23	12.2	10	17	16.9	30.9	2121	"
"	225	185	49	8	53.4	47	24	13.5	10.3	17.6	17.5	31.7	2129	"
"	216	182	47	17	53	46	23.5	13	10	17.5	17	32	2162	"
"	210	175	48	17	53	46	23	12	10.9	18	17	31	2174	"
"	213	173	48	19	53.2	45	22.1	11.6	10.5	17.2	17.2	—	2175	"

a large black or dusky patch on the chest, varying in size and sometimes extending to the throat and sides of the body, herein presenting a most interesting condition midway between typical *mentawi* and *melanogaster*; and the others practically agree with the type, but show some darkening of the reddish-brown of the chest: these phases are irrespective of sex. In no case could animals from Sipora and Siberut be confused.

15. *SCIURUS LOWII FRATERCULUS* Thomas.

S. fraterculus Thomas, 1895, p. 669: Sipora.

Sipora: 8♂, 5♀.

The series shows such a large degree of individual variation in the colour of the underparts that it would be almost impossible to use Thomas's original description as a means of comparison. The measurements given by him for his typical series are small, and those given by us below show that there is no difference in size between examples from Sipora, Siberut, and Pagi (*pumilus* Miller). The upper parts are remarkably uniform, but the range of variation below is considerable. Some specimens are strongly tinged with ochraceous from chin to vent; others have the chin and throat whitish. The grizzling of the flanks extends in most cases over the underparts, and in one specimen the whole of the underparts, except the head, may fairly be said to be grizzled slaty and buff. The hairs are always slaty at the base.

(For measurements see p. 825.)

16. *SCIURUS LOWII SIBERU*, subsp. n.

Type.—Adult female (skin and skull), collected on Siberut Island, West Sumatra, on 22nd September, 1924. Raffles Museum, No. 2056.

Characters.—Like *S. fraterculus* of Sipora, but with the underparts never strongly buffy or ochraceous. This is particularly noticeable on the throat, which in *fraterculus* is frequently rich ochraceous-buff.

Colour.—Upper parts, tail, and outer surface of the limbs finely grizzled buff and black, very uniform, but the buff slightly warmer on the posterior part of the body and on the tail. Inner sides of the limbs and underparts whitish, purest on the throat and the centre of the abdomen and sullied with grey, owing to the bases of the hairs showing through on the flanks and inner sides of the limbs.

Skull and teeth.—Exactly as in *fraterculus*.

Measurements.—See p. 825.

Specimens examined.—Fifteen, including the type.

Remarks.—As in *S. fraterculus*, the Siberut series is also variable below. One specimen is almost entirely white, others are faintly washed with buff, and in some there is a large amount of grizzling. Broadly speaking, six of the series agree with the type in having the whitish colour predominate below; the other

Sciurus lowii fraterculus (p. 824). *S. lowii siberu* (p. 824).

Species and Locality.	Sex.	Head and body.	Tail.	Hind foot.	Ear.	Skull.							Collector's No.	Remarks.	
						Greatest length.	Condylar length.	Palatal length.	Diastema.	Upper molar row.	Median nasal length.	Interorbital breadth.			Zygomatic breadth.
<i>Sciurus lowii fraterculus.</i>															
Sipora	♂	121	56	30	11.5	34	27.9	14.3	8	5.9	9.6	12	20.3	2201	Adult
"	♂	107	50	27	11	33	—	13.8	7.9	5.2	9	11.7	20	2315	"
"	♀	110	75	29	11	33.4	27.8	14.2	8	5.7	—	11.6	21	2316	"
"	♀	117	80	29	10	33.7	26.5	13.6	7.5	5.4	8.9	11	20	2356	"
"	♀	115	87	33	12	34	27.8	14.2	8	5.5	9.5	12.3	21.1	2412	"
"	♀	113	—	30	12	34	28	15	8.4	5.8	9	12	21.1	2420	"
"	♀	120	80	30	11	34	28	14.5	7.9	5.9	9.5	11.1	20	2211	"
"	♀	104	96	28	11	33.9	27.3	14.3	7.9	5.9	9.9	11.9	20.2	2230	"
"	♀	110	88	28	11	33.2	27.3	14	7.9	5.6	9.9	11	20	2384	"
<i>S. l. siberu.</i>															
Siberut	♂	118	79	30	11	33.5	28.1	14.6	8	5.5	9.1	11.5	20.5	2059	"
"	♀	119	72	30	12	33.5	27.6	14	7.5	5.9	9.7	11.1	20	2116	"
"	♀	110	80	29	12	34.6	28	15	8.9	5.5	10	12	21	2126	"
"	♀	113	72	29	12	34	28	14	7.9	5.9	10	11.9	20.6	2137	"
"	♀	115	90	29	12	33.7	27.6	14.2	8	5.5	9.8	11.2	21	2128	"
"	♀	116	80	30.5	11	33	27.5	14.5	8	5.9	9.5	12	21	2056	"

: Type.

nine are largely suffused or darkened with grey or brownish-grey, and some are not distinguishable from selected specimens from the Sipora series. None of the Siberut specimens shows the conspicuously ochraceous underparts of five in the Sipora series. The differences are, however, at the most average ones, and in some cases we should not care to identify individuals subspecifically. It can be said that while the two series overlap the extremes are most distinct.

S. piniensis and *S. balæ** from the Batu Islands seem on description rather different animals.

17. *LARISCUS NIOBE* OBSCURUS (Miller).

Funambulus obscurus Miller, Smith. Misc. Coll. xlv. 1903, p. 23, pl. i.: South Pagi Island.

Sipora: 16 ♂, 14 ♀.

Two species of this genus of ground-squirrel are known from Sumatra and the west coast islands—*niobe* and *insignis*. These have recently been discussed at length (*vide* Robinson and Kloss, Journ. F. M. S. Mus. viii. part 2, 1918, p. 37). As they occur side by side they must be regarded as species.

L. insignis (Sumatra) has the upper parts brighter and lighter, the underparts distinctly whitish, and larger bullæ.

L. niobe (Sumatra) has the upper parts duller and darker, the underparts, greyish and smaller bullæ.

No ground-squirrels of this genus were obtained by Modigliani on his visit to Sipora, but two forms have been described by Miller from the West Sumatran Islands.

L. rostratus (Miller, Smith. Misc. Coll. xlv. 1903, p. 24) from the Batu Islands seems from the description to be a form of *insignis*. As it has the underparts and inner surface of the legs cream-buff and the black stripes well developed, it does not require comparison with the specimens before us.

L. obscurus (Miller, *tom. cit.* p. 23, pl. i.) from South Pagi is said to have the dark lateral stripes obsolete and the underparts iron grey: it is a *niobe* form.

We have a topotype of *obscurus*, but it was mounted in 1903, and it is difficult to say to what extent it has faded.

For the present, therefore, we record the Sipora *Lariscus* as *obscurus*, with the description of which it agrees fairly well.

Miller's original description is not quite clear in one particular. For the characters of the Pagi form he gives "dark lateral stripes obsolete," and the type is described as "lateral stripes reduced to mere dark shades too indistinct to be measured or to have any definite colour"; but later this author states of the lateral stripes in four specimens out of seven, "nearly as well developed as the median stripe." His type was apparently an extreme, and not a typical example of the series. In the whole of our long series

* Miller, Smiths. Misc. Coll. xlv. 1903, p. 14.

we find that all three black stripes are readily distinguished, although not conspicuous and by no means comparable with those seen in the various forms of *insignis*, or in the typical *niobe*. As a series these specimens are surprisingly uniform above. The median line of the belly may be quite white, and the extent of this colour on throat and chest is very variable. Both this form and that next to be described differ from *n. niobe* (specimens examined from Korinchi, Sumatra) in their darker upper parts with less distinct stripes, less coarsely grizzled tail, and grey-white (non-buffy) underparts.

Both the Mentawi *Lariscus* have the skull-length in excess of that of *niobe* of Sumatra (*vide* Journ. F. M. S. Mus. viii. part 2, 1918, p. 41).

(For measurements see p. 828.)

18. *LARISCUS NIOBE SIBERU*, subsp. n. (Pl. IV. fig. 1.)

Type.—Adult male (skin and skull), collected on Siberut Island, West Sumatra, on 24th September, 1924. Raffles Museum, No. 2074.

Diagnosis.—A form of *niobe* closely resembling the Siporan *obscurus*, but with the black stripes absent or scarcely apparent.

Colour.—Above a very fine grizzle of black and light ochraceous, the muzzle and cheeks slightly greyer. Tail like the back, but the black predominating. Feet dark. Underparts and inner surface of the limbs grizzled iron-grey, becoming whitish on the chest and median line of the abdomen, the white varying in extent as in *obscurus*.

Skull and teeth.—As in *L. n. obscurus* (Miller).

Measurements.—See p. 828.

Specimens examined.—Seven males and seven females from the type-locality.

Remarks.—Although only differing from the Sipora form in a matter of degree, the Siberut animal is recognizable at sight, and side by side the series are very distinct. Looking down on the series, three of the males show indication of stripes, but only one as much so as the least heavily marked of the Sipora specimens. In others the markings have quite disappeared.

Mammæ: 3 pairs.

19. *RATTUS SABANUS SIPORANUS* (Thomas). (Pl. IV. fig. 2.)

Mus siporanus Thos. 1895, p. 670: Sipora.

Sipora: 10 ♂, 5 ♀.

Siberut: 1 ♂, 2 ♀.

These specimens agree well with the original description of *siporanus*. Sometimes there are dark isolated patches on the median line of the throat and abdomen, and these may fuse to form a long, narrow, median line on the underparts. The distal portion of the tail is always white. In two specimens the white areas are 100 and 140 mm. long. Seen from above the series

Lariscus niobe obscurus (p. 826).*L. niobe siberu* (p. 827).

Species and Localities.	Sex.	Head and body.	Tail.	Hind foot.	Ear.	Skull.							Collector's No.	Remarks.	
						Greatest length.	Condylar-basal length.	Palatilar length.	Diastema.	Upper molar row.	Median nasal length.	Interorbital breadth.			Zygomatic breadth.
<i>Lariscus niobe obscurus.</i>															
Sipora	♂	202	—	44	15	55	46	24	13.9	10.5	18.1	14.2	30.9	2203	Adult.
"	♂	192	98	43	15	53.5	45	23.5	13.6	10.9	17	14	29	2204	"
"	♂	155	65	44	16	54.4	—	24	14	10.5	17.6	14	30	2216	"
"	♂	205	80	44	16	54	45.1	23.8	14	11	18.5	13.1	29.3	2287	"
"	♂	205	90	43	17	54.1	44.9	23.7	14	10.6	17.2	13.9	29.8	2329	"
"	♂	194	88	43	15	53.2	44	23	13.8	10.5	17.1	14	28.4	2350	"
"	♂	203	80	41	16	52.1	44.3	23	14	10	17.4	—	—	2351	"
"	♂	206	100	43	15	53	44	23	13.2	10.5	16.6	—	29.5	2361	"
"	♂	210	85	42	16	52	44.3	22.9	13.1	10.5	17.8	—	29.5	2385	"
"	♂	200	100	43	16	53.9	45	23.9	14	10	17.3	—	29.6	2386	"
<i>L. n. siberu.</i>															
Siberut	♂	198	80	42	15	51.3	42.5	23	13	10.7	16.3	13.4	—	2034	" : Type.
"	♂	200	85	44.5	15.5	52.7	45	23	13.5	10.5	16.6	13.9	29	2047	"
"	♂	197	83	44	15	52.6	44.2	23.9	14	10	17.2	13.1	18.7	2074	"
"	♂	190	90	44	15.5	51	42.2	22.4	13	10.5	17.1	14	28	2079	"
"	♂	183	85	45	15	—	—	—	—	—	—	—	2098	"	
"	♂	189	86	45	14	52.1	—	23	14	10.2	16.1	14	30	2115	"
"	♂	220	77	45	15.5	53	44.2	22.9	—	—	16.8	—	30	2125	"
"	♂	196	—	42	15	52	43.1	23	13.4	10	16	14.1	29	2055	"
"	♂	195	80	44	14.5	52.1	44	22.5	13	10.5	16.1	—	—	2097	"

is very variable, some individuals being much more blackened than others: the palest animal is scarcely darkened at all except on the top of the head, a limited area on the rump, and the extremities of the limbs.

The dirty rufous-brown stain noted by Thomas is present in some, but this appears to be irrespective of sex: the two most strongly stained examples are females.

We cannot separate specimens from the two islands, but the series are very uneven. The three from Siberut are within the degree of nigrescence of the six darkest Siporan animals and darker than the rest of the latter. It seems possible that if we had a large series from Siberut, all would prove dark, and therefore indicate a distinct race. Miller has separated the Pagi Island form as *soccatus* (Smiths. Misc. Coll. xlv. 1903, p. 30) on account of the buffy non-rufous element of the upper parts.

Mammæ: 2 pairs pectoral, 2 pairs inguinal.

(For measurements see p. 830.)

20. *RATTUS SURIFER PAGENSIS* (Miller).

Mus pagensis Miller, Smiths. Misc. Coll. xlv. 1903, p. 39: South Pagi Island.

Mus rajah Thos. 1895, p. 672.

Sipora: 8 ♂, 9 ♀.

Siberut: 11 ♂, 28 ♀.

The spiny-backed rats from the two islands appear to us to be inseparable, and on description to be *pagensis*.

The series is large and admirably demonstrates the variability of characters frequently considered as of diagnostic value within this group. Comparatively speaking, the animals are very dark and uniform above, some being blackened from the muzzle to the root of the tail, although these, like the majority, still retain the tawny colour on the sides of the body and upper surface of the limbs. Normally, however, the dark saddle contracts to a narrow area on the rump, which is tawny and concolorous with the thighs. The great majority have a broad brown collar across the throat, but in some specimens there is not the slightest sign of a collar. The white of the underparts usually runs along the thighs as a narrow streak, becoming obsolete before reaching the heel, but in others the thighs are entirely brown. In a few examples the white is continuous, but by no means distinctly so, with the white of the hind foot. The tail is markedly white beneath, but the dorsal surface is invariably dark, and there is a universal absence of a white tip. No. 2013 (Siberut) has the pelage entirely white: tail bicolored, ears dusky, eyes black.

R. rarus (Rob. & Kloss *) from the Sumatran mainland is more brightly ochraceous, the tail light-tipped, and the collar

* Journ. Str. Br. Roy. Asiat. Soc. lxxiii. 1916, p. 272: Korinchi Peak, West Sumatra.

Rattus sabanus siporanus (p. 827). *R. swirfer pagensis* (p. 829).

Species and Localities.	Sex.	Head and body.	Tail.	Hind foot.	Ear.	Greatest length.	Skull.							Collector's No.	Remarks.
							Condyllo-basilar length.	Diameter.	Upper molar row.	Length of palatal foramina.	Median nasal length.	Breadth of combined navels.	Zygomatic breadth.		
<i>Rattus sabanus</i>															
Sipora	♂	260	300	52	28	55.1	48.1	15.91	10.5	8	22.2	5.9	26	2255	Adult.
"	♂	265	315	53	27	60	51.9	16.1	10.4	8.9	24	6	27	2258	"
"	♂	250	322	54	27	57.3	50.2	15.4	10.5	8.3	22.1	6	26.1	2262	"
"	♂	263	312	51	28	58.2	50.5	16.1	10.5	8	23.9	6.9	27	2267	"
"	♂	278	316	51	27	60.1	51.9	16	10.6	8	23.8	6.7	28.6	2277	"
"	♂	267	308	52	26	58	49.1	15.9	10.9	8.3	23.5	6.7	27.1	2392	"
"	♂	292	331	52.5	28	59.3	51.2	15.5	10.8	8.8	24.4	6.5	28.1	2392	"
Siberut	♂	270	323	52	27	58	49.9	16	10	8.1	23.7	6.9	26.9	2167	"
"	♂	270	—	52	30	60.9	52	16	11.2	9	25.3	6.5	—	2002	"
"	♂	264	319	54	27	56.2	49	14.7	10.8	7.4	22	6	26.1	2037	"
<i>R. swirfer pagensis.</i>															
Sipora	♂	185	176	42	21	47	38.5	12.9	7	7	18.4	5.1	21	2182	"
"	♂	210	200	43	21	46.3	39	12.6	7	7	18.5	5	20.2	2331	"
"	♂	198	177	44	23	48	40.1	12.7	7.5	7.3	18.4	5	21	2374	"
"	♂	202	185	42	24	49	40.3	13.1	7.6	7	19	5	21.5	2402	"
"	♂	203	—	43	21	48.6	40.9	13	7.3	7	19.9	5	22	2403	"
"	♂	182	177	41	21	47	38.2	12.1	7	7	18.4	5	20.9	2052	"
"	♂	200	165	41	—	43	39.5	12.7	7.1	7	18.9	5.5	20.4	2070	"
"	♂	206	178	44	23	48	39.5	13	7	6.5	19.8	5.2	21	2138	"
"	♂	210	190	41	23.5	47.5	40	12.8	7.1	6.3	18	6	21	2122	"
"	♂	210	178	44	—	47.9	40	13	7	6.7	19.2	6	21.3	2170	"

generally very bright and distinct; *catellifer* Miller* from Mansalar Island is another form with a white-tipped tail. The forms from the Batu Islands are bright and coarsely speckled †.

Mammæ: 2 pairs pectoral, 2 pairs inguinal.

(For measurements see p. 830.)

21. *RATTUS RATTUS MENTAWI*, subsp. n.

Type.—Adult male (skin and skull), collected on Sipora Island, West Sumatra, on 10th October, 1924. Raffles Museum, No. 2198.

Characters.—A rather coarsely grizzled rat differing from *lugens* ‡ of North Pagi Island in smaller size and apparently lighter colour, and from members of the *simulurensis* section in the possession of grey and not buff underparts.

Colour.—Back and sides grizzled black and ochraceous-buff, lightest on the sides: long black hairs of the upper parts iridescent. Outer side of the limbs and flanks hair-brown. Underparts smoky grey; an indistinct collar and median line of the chest broccoli-brown.

Measurements.—See p. 832.

Specimens examined.—Twenty males and fourteen females from Sipora; one male and one female from Siberut.

Remarks.—The type is the largest of the long series before us, none of which attain a skull-length of 51.4, as in the type of *lugens*.

One aberrant specimen (No. 2289) is uniformly brownish-black above and very dark grey below; several others, apparently in fresher pelage, are darker above than the type.

We cannot separate the two Siberut specimens from those collected on Sipora.

Mammæ: 2 pairs pectoral, 3 pairs inguinal.

22. *RATTUS RATTUS DIARDI* (Jentink).

Sipora: 3 ♂.

Siberut: 1 ♀.

Mammæ: 2 pairs pectoral, 3 pairs inguinal.

A house-rat, probably introduced.

(For measurements see p. 832.)

23. *TUPAIA GLIS CHRYSOGASTER* Miller. (Pl. V. fig. 2.)

T. chrysogaster Miller, Smiths. Misc. Coll. xlv. 1903, p. 58: North Pagi Island.

T. ferruginea hypochrysa Thomas, 1895, p. 665.

Sipora: 8 ♂, 11 ♀.

* Proc. U.S. Nat. Mus. xxvi. 1903, p. 464: Mansalar Island, West Sumatra.

† *E. pinacus* Miller, Proc. U.S. Nat. Mus. lli. 1916, p. 460, Pinie Island; *E. mabalus* idem, ibid. p. 449, Tana Masa Island.

‡ Miller, Smiths. Misc. Coll. xlv. 1903, p. 38.

Rattus rattus mentawi (p. 831). *R. rattus diardi* (p. 831)

Species and Locality.	Sex.	Head and body.	Tail.	Hind foot.	Ear.	Skull.								Collector's No.	Remarks.
						Greatest length.	Condylar-basilar length.	Diastema.	Upper molar row.	Length of palatal foramina.	Median nasal length.	Breadth of combined nasals.	Zygomatic breadth.		
<i>R. rattus mentawi.</i>															
Sipora	♂	214	—	42	23	48.5	42.3	12.9	9	8.1	18.6	5.5	22	2177	Adult.
"	♂	212	206	38	23	47.6	42	13.3	7.5	8.5	19	6.3	21.5	2178	" : Type.
"	♂	209	230	39	23	49.9	43.2	14.3	—	8.9	19.5	5.5	21.8	2198	"
"	♂	215	217	39	23	45.6	43.3	14.1	8	9.4	19.2	6	22.1	2247	"
"	♂	207	226	41	24	47.6	42	13.2	—	8.2	18	5.5	21	2259	"
"	♂	203	208	38	23	47	41.1	13.8	8	8.9	18.2	5	22	2260	"
"	♂	201	211	37	22	47.4	42	13	8.9	8.3	18	5.5	22.6	2260	"
Siberut	♂	206	210	40	24	49	42.5	14	7.9	8.8	18.5	5.1	22	2322	"
"	♂	206	210	38	22	48	41.1	13.1	8.3	8	19	6	21.7	2124	"
"	♂	206	210	38	22	48	41.1	13.1	8.5	8.2	18	5.2	22.1	2301	"
<i>R. r. diardi.</i>															
Sipora	♂	194	218	35	20	42.8	38	12.3	7	8	16	5	20	2273	"
"	♂	173	174	33	20	41.2	36.5	11.5	7	8.2	15.5	4.9	19	2324	"
"	♂	197	197	35	20	41.4	37	—	7	—	15	5	20.5	2347	"
"	♂	178	191	38	21	43	37.6	12	6.9	7.2	15.1	5	19	2048	"

In 1895 (*l. c. s.*) Thomas described a golden-chested *Tupaia* from Java as *hypochrysa*, and identified with it two females from Sipora, stating, however, that their tails were greyer than the type of his new form. Later, Lyon in his monograph of the *Tupaiaidæ* (Proc. U.S. Nat. Mus. xlv. 1913, p. 79) placed two Sipora specimens with *chrysogaster* described from the Pagi Islands.

(The inclusion of Nias in the range of *chrysogaster* in the key given by Lyon, *tom. cit.* p. 39, is no doubt a slip, as no mention of this island is made elsewhere under *chrysogaster*.)

Mammæ: 1 pair only (median).

(For measurements, see p. 834).

24. *TUPAIA GLIS SIBERU*, subsp. n. (Pl. V. fig. 1.)

Type.—Adult male (skin and skull), collected on Siberut Island, West Sumatra, on 22nd September, 1924. Raffles Museum, No. 2058.

Diagnosis.—Like *T. chrysogaster* from Sipora, but duller; the neck stripe and grizzling of the upper parts nearer tawny-ochraceous than ochraceous-rufous.

Skull and teeth.—Essentially as in *chrysogaster*.

Measurements.—See p. 834.

Specimens examined.—The type and three others, all from Siberut.

Remarks.—This is a good form, recognisable at sight, although not strikingly different from the Sipora animal. The underparts are within the range of *chrysogaster*, but no specimen in the small series reaches the brilliancy of colour attained by some of the nineteen from Sipora.

25. *PTEROPUS HYPOMELANUS ENGANUS* Miller.

Pteropus enganus Miller, Proc. U.S. Nat. Mus. xxx. 1906, p. 822: Engano.

Pteropus hypomelanus Thomas, 1895, p. 664.

Sipora: 4 ♂, 5 ♀.

Siberut: 1 ♂.

The measurements of this series agree closely with those given by Andersen (Cat. Chir. Brit. Mus. 1912, pp. 108 and 112) for *enganus*, forearm 121–133.5 mm. Furthermore, we have examined two topotypes of *enganus*, and although these are not in the best of condition, we can perceive no difference between them and the Mentawi material.

P. h. simalurus Thomas (Ann. Mag. Nat. Hist. (9) xii. 1923, p. 592), from Simalur, is another form belonging to that section of *hypomelanus* having the crown and sides of the head generally similar in colour to the back, but it is large, with a forearm of 141–149 mm.

The mantle shows considerable variation in colour, but it should be noted that three specimens not marked as adult agree

Tupaia glis chrysogaster (p. 831). *T. glis siberu* (p. 833).

Species and Locality.	Sex.	Head and body.	Tail.	Hind foot.	Ear.	Skull.							Collector's No.	Remarks.
						Greatest length.	Basal length.	Palatal length.	Upper molar row (alveoli).	Tip of premaxilla to lachrymal notch.	Nostril breadth at diastema.	Interorbital breadth.		
<i>Tupaia glis chrysogaster.</i>														
Sipora	♂	185	138	43	16	53	45.5	28	19.5	22	7.1	14	26.6	2229 Adult.
"	♂	177	145	43	14	55	46.5	29.3	19.2	24.5	7.1	15.5	28	2327 "
"	♂	193	157	46	15	57	48	30.2	20.5	24.6	7.9	15	28	2394 "
"	♂	196	150	45	14	56.5	48.5	31	20.6	25.1	7	15.5	27	2324 "
"	♂	204	156	45	16	56.3	47.5	30	21.4	24.5	7.5	15	28.9	2368 "
"	♂	205	143	43	15	58	49.5	31.5	21	26.1	7.8	—	27.4	2269 "
"	♂	183	142	—	15.5	—	47	20.2	20.6	24	—	15	17	2274 "
"	♂	188	147	44	15	55	47	29.1	21	24.3	6.9	14.2	27.7	2290 "
<i>T. g. siberu.</i>														
Siberut	♂	196	156	44.5	14.5	50.2	—	30.9	21	25.7	7.5	15	26.7	2058 " : Type.
"	♂	195	145	44	15	54	45.9	28.5	—	—	—	14.5	—	2172 "
"	♂	—	—	—	—	—	—	—	20.5	24.9	7.3	—	—	2139 "
"	♂	—	—	—	—	54.2	46.9	29.8	20.1	24.2	7.5	14.6	26.5	2147 "

Pteropus hypomelanus enganensis (p. 833). *P. rampyrus malaccensis* (p. 836).

Species and Locality.	Sex.	Head and body.	Tail.	Hind foot.	Tibia.	Ear.	Forearm.	Skull.							Collector's No.	Remarks.		
								Greatest length.	Condylar-basal length.	Basal length.	Palatal length.	Rostrum orbit to nares.	Least interorbital breadth.	Maxillary tooth row, excluding incisors (alveoli).			Zygomatic breadth.	Mandible from condyle.
<i>Pteropus hypomelanus enganensis.</i>																		
Sipora	♂	187	—	41	—	23	118	61	59.5	—	32.9	18.9	21.9	8.1	—	45.7	2191	Adult.
"	♂	193	—	42	—	24	118	53.7	—	55.5	35.1	19.5	22	8	30	45.3	2222	"
"	♀	158	—	40	—	23	112	61.5	—	45.3	30	17	20.7	7.5	25.5	40	2225	Immature.
"	♀	214	—	38	58	24	134 (+)	53	62	58	37	21.5	23.7	8.3	33	51	2305	Adult.
"	♀	157	—	36	—	21	110	53	50.4	46.5	29.5	—	20.5	7.5	28	40	2178	Immature.
"	♀	200	—	39	—	25	128	62.4	60.5	56.2	—	19.5	—	9	31	49	2192	Adult.
"	♀	203	—	39	—	23	133	65	52	48	31	17.5	21.5	7.7	28	42.5	2193	"
"	♀	170	—	37	—	24	118	55	52	—	35.5	18.7	23	8.1	30	49	2194	Subadult.
"	♀	197	—	34	58	25	131 (+)	62.2	—	—	37.4	21	24.9	8.2	35.9	51	2278	Adult.
Siberut	♀	218	—	41	—	25	134	65	62.9	58.2	—	—	—	—	—	—	2135	"
<i>P. vampyrus malaccensis.</i>																		
Sipora	♂	320	—	58	95	41	195	80.5	80	74.6	44.8	26.1	—	31.4	44.5	64.5	2266	"
"	♂	280	—	57	95	43	200	79.5	79	73.2	45.9	26	—	30.5	43	63.4	2416	"

among themselves and differ from the remainder in having the mantle ochraceous-buff, whereas in the others it is much richer, near chestnut.

(For measurements see p. 835.)

26. *PTEROPUS VAMPIRUS MALACCENSIS* K. And.

Pteropus vampyrus Thomas, 1895, p. 664.

Sipora: 2 ♂.

This species has been hitherto unrecorded for the West Sumatran Islands. One of the specimens is in every respect a normal *malaccensis*, but the other has the rostrum, teeth, palate, and interpterygoid space much narrower than usual.

(For measurements see p. 835.)

27. *CYNOPTERUS ANGULATUS* Miller.

Cynopterus marginatus Thomas, 1895, p. 664.

Sipora: 2 ♂, 1 ♀; 19 specimens in alcohol.

Siberut: 2 ♂, 2 ♀.

A small *Cynopterus* was described from North Pagi by Miller (Proc. Biol. Soc. Wash. xix. 1906, p. 62) as *pagensis*, but Andersen (Cat. Chir. Brit. Mus. 1912, p. 613) reduces this name to a synonym of *angulatus*. Andersen examined paratypes of *pagensis* and also two specimens from Sipora.

The small series of skins before us shows the wide range of colour usually seen in these small fruit-bats.

The specimens in alcohol all have the long forearm of *angulatus*.

(For measurements see p. 837.)

28. *MACROGLOSSUS MINIMUS FRATERNUS*, subsp. n.

Type.—Adult female (skin and skull), collected on Sipora Island, West Sumatra, on 25th October, 1924. Raffles Museum, No. 2342.

Diagnosis.—Like *M. m. sobrinus** but larger. Forearm 49–52 (42–48·5)†; skull, lambda to gnathion 31·5–32·9 (28·5–29·5); rostrum 12–13 (9·5–10·5); mandible from condyle 25·3–26 (21·2–22·7).

Measurements.—See p. 837.

Specimens examined.—Two adults (including the type) and one juvenile from Sipora; one adult from Siberut.

Remarks.—As *M. m. sobrinus* is larger than *M. m. minimus* of Java, so this form is larger than *sobrinus* of the Malay Peninsula, Sumatra, and Java.

The juvenile is rather duller or darker in colour than the adults of the small series before us, in only two of which can we detect that the head is very slightly darker than the rest of the upper parts.

* Andersen, Ann. Mag. Nat. Hist. (8) vii. 1911, p. 642.

† Measurements in parentheses are those given for *sobrinus* (Anderson, Cat. Chir. Brit. Mus. 1912, p. 767).

Cynopterus angulatus (p. 836). *Macroglossus minimus fraternus* (p. 836).

Species and Locality.	Sex.	Skull.										Collector's No.	Remarks.					
		Head and body.	Tail.	Hind foot.	Tibia.	Fur.	Forearm.	Greatest length.	Condylar-basal length.	Basal length.	Palatal length.			Rostral orbit to nares.	Least interorbital breadth.	Maxillary tooth row excluding incisors (alveoli).	Zygomatic breadth.	Mandible from condyle.
<i>Cynopterus angulatus</i> .																		
Sipora	♂	100	11	16	—	16	69	31.7	30.1	—	16.4	7.8	6	10	—	23.5	2306	Adult.
"	♂	106	12	14	26	16	73	32.6	31	28.3	16.1	7.9	6.7	10.3	—	24.4	2363	"
"	♀	95	10	15	22	16	66	30.1	29	26.9	16	7.5	6.6	10.1	19	23.2	2325	Subadult.
Siberut	♂	104	10	—	—	18	71	—	32	—	17.2	8	7	11	20.9	25.2	2186	"
"	♂	105	12	—	—	18	—	32	31	28.9	17	7.9	6.7	10	22	24.2	2158	"
"	♀	98	10	—	—	16	68	31	29.2	27	17	7.7	—	10	—	23	2137	"
"	♀	92	9	14	—	16	63	30	29	26.3	16	7.2	6	10	—	22.9	2166	"
<i>Macroglossus minimus fraternus</i> .																		
Sipora	♀	88	—	12.5	—	14	52	31.9	30	28.1	18.2	12.6	5.9	10	17	25	2240	Adult.
"	♀	90	—	12	20	16	52	32.9	30.6	28.5	18.5	13	5.8	10.2	—	26	2342	" : Type.
Siberut	♂	83	4	14	—	16	49	31.5	29.1	27.1	17.3	12	5.3	10.6	16.9	25.3	2042	"

No. 2042 was noted by the collector as having the membranes and feet a darker brown than the ears and back, and No. 2240 as brown throughout with the finger-bones crimson.

The specimen recorded from Nias as *sobrinus* by Andersen * is immature and may belong to the present form.

29. *EMBALLONURA MONTICOLA MONTICOLA* Temminck.

Emballonura semicaudata Thomas, 1895, p. 695.

Sipora: 1 ♂ (skin); 4 specimens in alcohol.

Siberut: 27 specimens in spirits.

These bats seem identical with a series from Pahang, Malay Peninsula (*E. peninsularis* Miller, Proc. Acad. Nat. Sci. Phil. 1898, p. 324). In colour the skin agrees very well with the description given by Miller for *peninsularis*. The collector notes that one specimen had the throat brighter than the rest of the underside. The large series in alcohol agrees closely in dimensions with those recorded below.

(For measurements see p. 839.)

30. *MYOTIS MURICOLA* (Gray).

Sipora: 1 ♂, 2 ♀ (in alcohol).

These three specimens may represent *M. abbotti* Lyon (Proc. U.S. Nat. Mus. lii. 1916, p. 441) from North Pagi Island.

They were noted by the collector as being blackish-brown, black, or dark brown above; and black (or paler) below, with the hairs tipped with whitish. Wing-membranes black.

(For measurements see p. 839.)

31. *KERIVOULA HARDWICKII* ENGANA Miller.

Kerivoula engana Miller, Proc. U.S. Nat. Mus. xxx. 1906, p. 825: Pulau Dua, Engano.

Kerivoula hardwickii Thomas, 1895, p. 665.

Sipora: 1 ♀ ad., 1 juv.

Siberut: 1 ♂ imm., 2 ♀ ad.

Kerivoula engana, forearm 33-34.4 mm., was described as being larger than *hardwickii* of Java, which (*vide* Thos. & Wr. P. Z. S. 1900, p. 382) has the forearm 31-33 mm. The forearms of our adult series are 33, 35, 36 mm. The measurements of the skulls before us are also in close agreement with those of the type of *engana*, and thus, on size, the Mentawi animal seems to belong to the Engano race.

No. 2072 of the present series was noted as dark brown above, paler brown below. Nos. 2073 and 2017 were stated to be blackish-brown above, with the hairs of the underparts tipped

* Cac. Chir. Brit. Mus. 1912, p. 761.

Emballonura monticola (p. 838). *Myotis muricola* (p. 838).
Kerivoula hardwickii (p. 838).

Species and Localities.	Sex.	Head and body.	Tail.	Hind foot.	Tibia.	Ear.	Forearm.	Skull.								Collector's No.	Remarks.	Subadult.		
								(Greatest length.	(Ondylo-basal length.	Basal length.	Palatal length.	Least interorbital breadth.	Mustoid breadth.	Maxillary tooth row, excluding incisors (alveoli).	Zygomatic breadth.				Breadth of brain-case.	Greatest length of mandible.
<i>Emballonura m. monticola.</i>																				
Sipora	♂	47.5	13.5	8	14.5	15	43	—	—	—	—	2.9	7.2 (+)	4.1	8.7	7	9.7	2313		
Siberut	♂	47	13	8	17	14	45	14.2	13	11.5	5.5	2.9	7.5	6	8.1	6.9	10	2068		
"	♂	48	11.5	—	16	15	43	14	12.9	11.3	5.1	2.9	7.5	5	8.3	7	9.8	2075		
"	♂	45	12.5	—	16	13	45	14.6	13	11.6	5.3	2.8	7.1	5	8.9	7	9.9	2113		
"	♂	46	13	7	17	13	44	14.9	13.6	11.8	5.6	2.9	7.9	6	—	7	10	2114		
<i>Myotis muricola.</i>																				
Sipora ..	♂	46	41	—	—	14	35	14.2	13.4	12.1	7.1	3.6	7.1	5.8	—	6.8	10.5	2091		
"	♂	44	44	—	—	13	35	14.1	13.4	12	7.5	3.7	7.2	5.5	9.2	6.9	10.6	2082		
"	♂	39	39	—	—	12	31	13.6	12.5	11.2	7	3.6	7.2	5.2	—	7	10.1	2166		
<i>Kerivoula hardwickii engana.</i>																				
Sipora ..	♂	40	43	—	—	14	36	14.3 (+)	14	12.4	8.5	3.1	8	0	9.2	7.5	11.1	2238		
Siberut ..	♂	30	33	—	—	13	29	13	12	10.6	6.3	3	7	5	—	7.2	9	2073		
"	♂	39	42	8	—	13	33	14	13.2	12	8	3.1	7.5	5.8	—	7.5	10.3	2017		
"	♂	48	46	—	—	15	35	14.9	13.6	12.2	8.3	3.1	7.9	5.9	9.3	7.9	11	2072		

buffy or albescent. Membranes black. The juvenile was dusky or black above, slightly grey below, mostly on the median line and abdomen.

(For measurements see p. 839.)

EXPLANATION OF THE PLATES.

PLATE I.

Pithecus potenziani siberu.

PLATE II.

Simias concolor siberu.

PLATE III.

Fig. 1. *Sciurus melanogaster melanogaster.*

2. *Sciurus melanogaster mentawi.*

3. *Sciurus melanogaster atratus.*

PLATE IV.

Fig. 1. *Lariscus niobe siberu.* $\frac{1}{2}$ nat. size.

2. *Rattus sabanus siporanus.* $\frac{1}{4}$ nat. size.

PLATE V.

Fig. 1. *Tupaia glis siberu.*

2. *Tupaia glis chrysogaster.*

42. Field Observations on Spider Mimics.

By Major R. W. G. HINGSTON, I.M.S., F.Z.S.

[Received October 14, 1927: Read November 1, 1927.]

(Text-figures 1-10.)

Many spiders live with and mimic ants. The mimicry benefits the spider in two ways. First, it gives protection to the mimic by concealing it in the midst of the ants. Second, it has an aggressive value; for many of these mimics, at least in India, habitually attack and feed on their models. The ants, therefore, both protect their mimics, and at the same time supply them with food. Numerous examples are met with in India. This paper is a study of their habits and behaviour, in so far as concerns their relationship with the ants. Only by such observations made in the field can we understand the purpose that mimicry fulfils.

I am much indebted to M. Louis Fage for examining my specimens of spiders. It is difficult to identify small tropical spiders. In many cases the genus only can be established. Such identifications, however, as are given in this paper, have, at least, the support of M. Fage's authority.

Observed at Fyzabad in Central India.

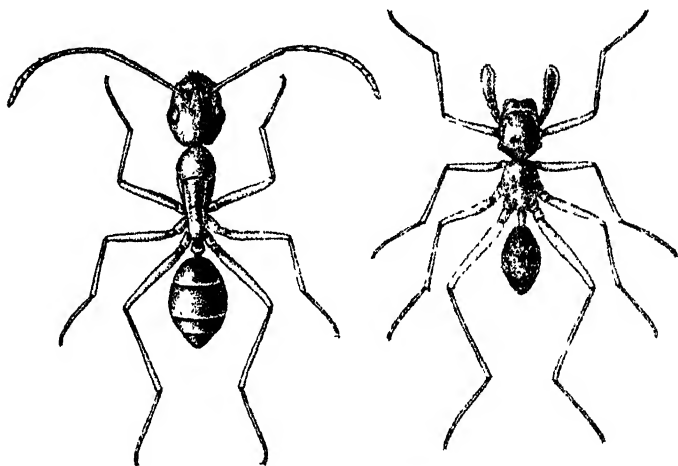
The large Indian black ant, *Camponotus compressus*, is one of the most common insects of the plains. It nests on the ground, usually at the foot of a large tree. Workers are continually issuing from the nest and ascending the tree to explore the branches. The mimic of this ant is a *Myrmarachne*, probably a new species, and very near *M. bifurcata*. I have found it on the fig, the dhak, the mango, and other trees, keeping company with the worker ants.

A few remarks on points of anatomical resemblance. The mimic is the size of an intermediate worker. It is of the same uniform black colour and slender elongated shape. Model and mimic have squarish heads, the same arched type of thorax, the same long slender legs. Each has a narrow constricted waist, in each the abdomen is uniformly oval and has a bright superficial gloss. The pedipalps of the mimic, when bent beneath its head, look very like the ant's jaws. The most interesting feature in the resemblance is the way the spider simulates antennæ. In ants the antennæ are conspicuous organs, thrust out in front and kept continually in motion. The mimic employs its front pair of legs in order to simulate the antennæ of its model. It does not use them for ordinary progression. They

are thrust forward, bent into a right angle—in fact, made to occupy a position similar to that of the ant's antennæ. Moreover, their tips are kept continually in motion, a striking feature, for it is not just an aimless movement, but rather that methodical swaying motion so characteristic of *Camponotus* ants. I defy anyone, when watching this mimic and particularly observing these false antennæ, not to be amazed at this wonderful resemblance between the mimicking spider and the ant.

These mimics live on the open foliage and construct silk shelters in the hollow of leaves. Their habits are as ant-like as their structure. The worker ants, as a rule, move quietly through the foliage in a steady searching kind of way. When

Text-figure 1.



Ant. *Camponotus compressus* Fabr.

Spider. *Myrmarachne* sp.

alarmed, however, they rush about excitedly. The mimic also simulates these motions exactly. Its ordinary progression is steady and even. But the moment it is disturbed its behaviour changes. Then it assumes the bustle of the workers, simulates their rapid jerky gait, perhaps darts for safety underneath a leaf or escapes by a sudden spring. The ants are graded into different sizes, a fact which is clearly advantageous to the mimic by enabling it to simulate different castes at successive stages in its growth. Another habit of *Camponotus* ants is to erect the abdomen at right angles to the body and walk about with it thrust into the air. And this same peculiar attitude is sometimes assumed by the mimicking spider.

This close resemblance in the behaviour of mimic and model

has been observed in the case of other species of *Camponotus*. Pocock makes mention of a spider-mimic almost indistinguishable from the female of *Camponotus opaciventris*. The ant moves by a series of rushes and pauses, and this peculiar mode of progression is imitated closely by the spider. Messrs. Myers and Salt refer to a Clubionid spider which mimics *Camponotus planatus* in Cuba. They point out that the gait of the spider is indistinguishable from that of the ant; also that the spider uses its first pair of legs for the purpose of simulating the ant's antennæ.

This close resemblance both in structure and habit must be of protective value to the mimic. But I have notes that suggest an aggressive function. These mimics lie in ambush for the ants. Waiting for a chance, they sit quietly on a stem or conceal themselves in clefts between the leaves. They will not attack a vigorous ant: rather they jump back if one approaches. But if the mimic can get in an advantageous position it will make a sudden pounce on its model, throw it on its back, and grip it by the neck. If the ant is examined immediately afterwards it will be found to be paralysed but not quite dead. Poison has been injected by the mimic, probably into the cervical ganglion of the ant. Hence the aggressive value of the mimicry. It enables the mimic to mix with its models and to pounce on them without being seen.

Observed at Fyzabad in Central India.

Camponotus paria is another widespread species in India. It differs distinctly from *C. compressus*, being shorter, more stumpy, and covered with a silky gloss. It frequents vegetation and nests on the ground.

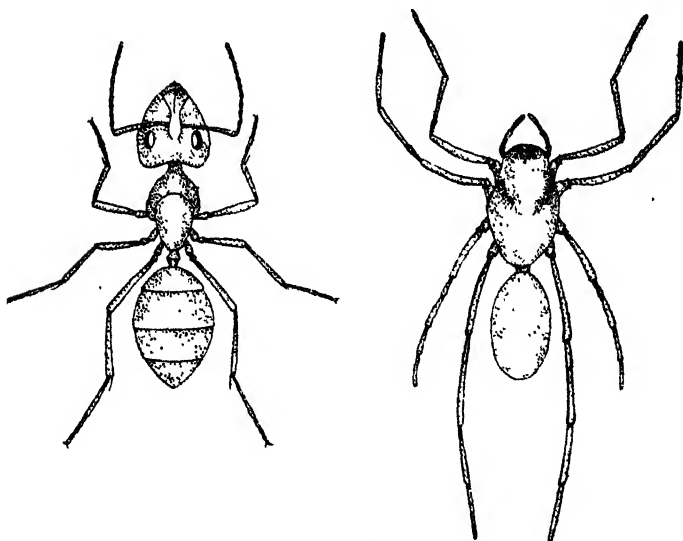
Its mimic is a species of *Castaneira*. Like most of those mentioned in this paper, it belongs to series 2 of Mr. Donisthorpe's classification, that is to those species which hunt and prey on ants and are generally found outside and in the neighbourhood of the nests.

The resemblance in anatomical structure is not nearly so close as in the last example. There is one point, however, of special significance. *C. compressus* is uniformly black; *C. paria* is covered with a silky lustre, spread evenly over the thorax and in greyish rings around the abdomen. The same difference applies to the mimics. The *compressus* mimic is glossy black; there is not a trace of fur. The *paria* mimic has a silky covering, somewhat patchy, but very like the fur on its model. On the thorax it is spread fairly evenly, but arranged in bands on the abdomen quite like the rings round the abdomen of the ant.

Now for the offensive value of the mimicry. At sunset these ants retire to the formicary. They move in a slow methodical stream. This is the opportunity for the mimics. At sunset they grow active, hunt about with greater eagerness, ascend

stems, explore under leaves; many emerge from hiding-places beneath debris and prowl about close to the nest. All the time

Text-figure 2.



Ant. *Camponotus paria* Emery.
Spider. *Castaneira* sp.

they are on the watch for a worker-ant that has straggled from the main stream. A chance offers. There is a sudden rush. The ant is seized, carried off, and the body-fluid is sucked out.

Observed at Fyzabad in Central India.

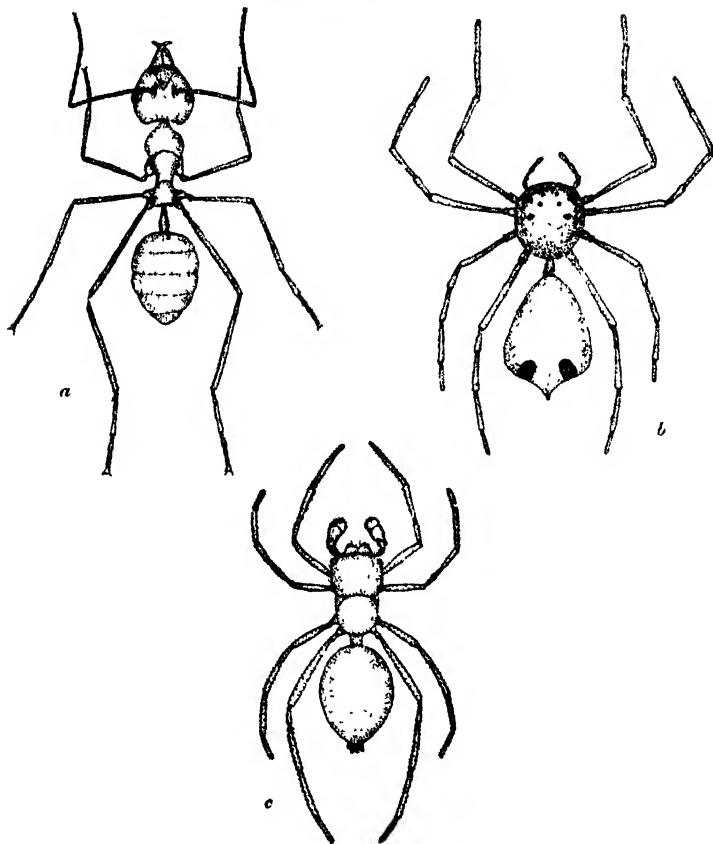
The red ant is extremely common. It is a tree-haunting species, nesting in the foliage, and despatching columns along the branches and down the trunk of the tree to the ground.

Two quite different species of mimicking spiders are frequently seen in the company of these ants. Sometimes they move in the midst of the columns; at other times they explore the foliage or debris at the foot of the trees. The species are *Amyciaea forticeps* or a closely-allied species, and a species of *Myrmarachne* very near *M. plataleodes* Cl.

My remarks refer to *A. forticeps*. The anatomical resemblance between this mimic and its model has been carefully described by Pocock. The point of particular interest is that at the end of the spider's abdomen are two conspicuous black spots, while there are no such spots at a corresponding position on the abdomen of the ant. Their place in the scheme of mimicry has been explained by twisting the spider round so that its tail corresponds

to the ant's head and the two black spots to the ant's eyes. Pocock writes: "The high and rounded cephalothorax of this spider represents the abdomen of the ant, the waists of the two correspond, and the long, constricted abdomen of the spider with the large black spots at the end, imitate the thorax, head, and

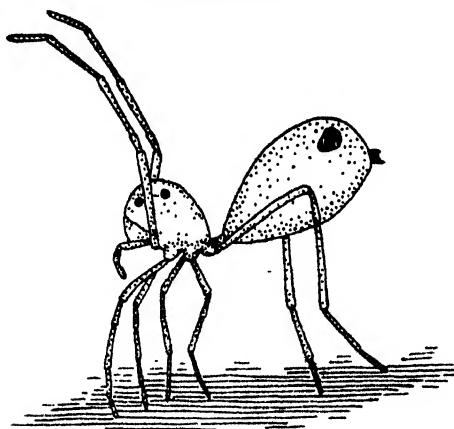
Text-figure 3 (a-c).

(a) Ant. *Oecophylla smaragdina* Fabr.(b) Spider. *Amyciaea* sp.; and (c) *Myrmarachne* sp.

two eyes of the ant. Thus the posterior end of the spider corresponds with the anterior end of the ant, an anomaly, no doubt, connected with the habit, so characteristic of the Thomisidæ, of moving sideways and backwards with almost greater facility and frequency than forwards."

This explanation may be the correct one. I did not know of it when I met with these mimics, and at the time made a different surmise as to the purpose of these black spots. It is true that at a corresponding point on the ant's abdomen there is nothing to compare with these two black spots. But when an *Ecophylla* worker is alarmed it elevates its abdomen, bends it over its back, until the under surface is fully exposed. Then we notice that on the middle of the under surface of the ant's abdomen is a conspicuous black patch. It is clearly visible from behind, but only when the abdomen is raised. Now the spots at the end of the spider's abdomen correspond with this black patch. Anatomically they occupy different positions. But the spider does not habitually hoist forward its abdomen in the manner so

Text-figure 3 (d):

Alluring attitude of *Amyciaea*.

characteristic of these ants. Hence, the best attempt at resemblance is secured by having the spots at the extreme end.

I come to some observations on the mimic's behaviour. It haunts the foliage, also the debris underneath the tree. Amongst the leaves it makes a silk shelter from which it emerges to attack the ants. There is no haste about its ordinary movements. It crawls about quietly in the same way as the workers, its front legs mocking antennæ exactly. The ants have a habit of exploring the foliage by crawling around the edges of the leaves. The mimic does precisely the same. If disturbed, however, its method changes. It hustles about just like the ants, and moves, like them, in a quick run. When alarmed, it often darts to the under surface of a leaf, or slinks for concealment into a crevice, or drops down upon a thread. Its attitudes

and gesticulations make the mimicry complete. The mimic in its prowls makes momentary halts. Up goes its legs like a pair of antennæ. It has a knack of bringing them together, giving them a particular elbow-bend so as to make them look like ant's antennæ springing from the sides of its head. Their tips at the same time are thrust into the air, and head and thorax are raised from the leaf. This results in a most uns spider-like attitude. The front part of the body is erect, the hind part lowered. It makes the mimic almost identical with its model, for the red ants always assume this attitude whenever they are angry or disturbed.

I have seen this mimic attacking its models. The spider wanders about the leaves, moving circumspectly, watching for a chance. It does not care to get into the midst of the workers. It hangs along the outskirts of their column watching for one that has wandered from the file. An opportunity comes, and I see the following act take place:—The mimic climbs on to a leaf and halts. Then it raises its abdomen, erects its antennæ, and thus assumes the attitude of an alarmed ant. A worker approaches (and the workers of *Ecophylla* have sharp powers of vision), it comes on to the leaf, sees the spider in this alarm attitude, becomes apprehensive and comes to a halt. This gives the mimic a chance. It turns about, runs towards the worker, manoeuvres so as to approach it from behind, then advances more quietly, and springs back alarmed. Obviously the attack is dangerous for the mimic. It makes a second advance, comes warily to the tip of the ant's abdomen, then suddenly with a spring throws itself on its model's back. A swift momentary tussle follows, and the ant is dead. The mimic then drags it underneath a leaf.

We note the part that the false antennæ play in these peculiar uns spiderlike gesticulations. This point seems to me of importance with respect to the view, previously mentioned, that the spider corresponds to an ant turned the wrong way round. If the spider's abdomen corresponds to the head of the ant, the black spots on it to the ant's eyes, and the spider's head to the ant's abdomen, then we can no longer regard the front legs as simulating antennæ for they will be situated at the wrong end. Yet nothing is more clear in these gesticulations than that the erection, the elbowing, and the quivering of the spider's first pair of legs are the very image of the antennæ of the ant.

Thus these mimics live on their models. The mimicry enables them to approach their prey. Indeed, their behaviour is a kind of lure to the ants. When a red ant halts and elevates its body, this implies that it suspects danger, and other ants seeing the attitude come to a standstill. The mimic makes use of this characteristic. It halts and simulates the alarm attitude. A worker, seeing the mimic, takes it to be another ant making the ordinary danger signal. It, too, halts. This gives the mimic its chance. For when the model is standing still the mimic can

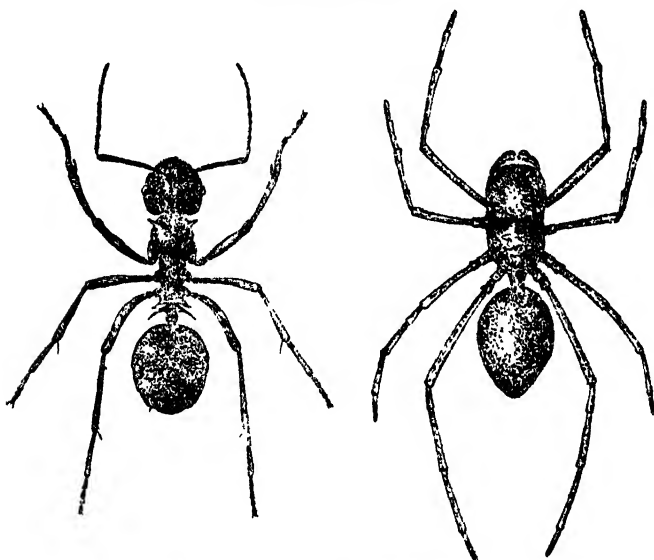
manœuvre, can work round to the rear of the ant, and thus get into position for a spring.

Observed at Fyzabad in Central India.

Polyrhachis simplex makes a nest of débris and silk either at the foot of, or in the branches of, a tree. It sends columns into the foliage which break up in search of Membracids.

I met with its mimic only once. A nest of these ants was in a bush of tamarisk. Near it was a group of four workers trying to get juice from a membracid. An inch from them was what seemed to be a fifth worker. Not till it moved did I detect it as a mimic. Clearly it was stalking the ants.

Text-figure 4.



Ant. *Polyrhachis simplex* Meyr.

Spider. *Myrmarachne* sp.

The spider is a species of *Myrmarachne*. Again we see the close anatomical resemblance, in size, colour, shape, build, slender legs, narrow waist, constriction across spider's cephalothorax, its front legs thrust out like ant's antennæ, its abdomen covered with a silky gloss, which is characteristic of these *Polyrhachis* ants.

At intervals the mimic approached the group of workers. It crept forward stealthily, opened its jaws, and seemed as though about to make a spring. It was obvious that the mimic feared its model. When an ant approached, the mimic moved aside,

then dodged behind a stem. Like all these mimics its movements were wary. At the slightest alarm it rushed into some shelter. When not engaged in hunting it kept underneath a tent of silk. There is little doubt that it waits for an opportunity to spring on an unsuspecting ant.

The combination of timidity and rapacity in these mimics resembles that shown by staphylinid beetles which so frequently inhabit the interior of ants' nests. *Myrmedonia* and *Tapinoma* seem particularly destructive. Wheeler describes how they lurk about the nests, capture solitary or disabled workers, or kill them at night when they are overcome with the cold. The ants rush at them, but the beetles start back, emit a dangerous excretion, and escape. The relationship is not unlike that between the spider-mimics and the ants. Ants display the same hostility to crickets of the genus *Myrmecophila* which live with them on such intimate terms in the nest. Wheeler tells how he watched the *Myrmecophila* nibbling at the secretions on the ant's body, how the ant made a lunge at its unwelcome guest, and how the cricket with a spring was far away by the time the jaws of the ant had closed. Thus other kinds of guests besides these spider-mimics have to keep continually on the alert and be ready in an instant to spring into security if approached too closely by one of their hosts.

Observed at Baghdad.

Messor barbarus, the harvesting ant, is very abundant in Mesopotamia. It makes a nest in the soil, and moves along paths which run between the harvesting area and the nest.

One evening I saw what looked like a deformed ant moving about in the swarm of harvesters. Not till after I had captured it did I find that it was a spider which looked very like one of the ants. I then examined all the nests in the neighbourhood and found that at quite half of the nests one or two of these spiders were established.

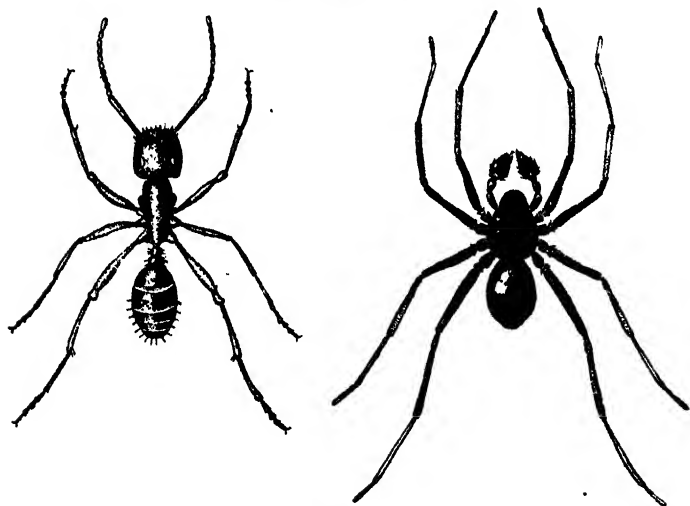
The mimic belongs to the genus *Zodarion*. It is about the size of one of the larger workers. In general build it is stouter and more stumpy: but its legs are long and slender; and its dark thorax and glossy black abdomen are the same colour as those of its model. Its movements are not unlike those of the harvesters but appear somewhat more hasty. When alarmed, it crouches amidst the débris of the nest, lies motionless, shamming death, and becomes indistinguishable in the midst of the harvesters. I seldom found more than one spider at a nest. It always lurked close to the entrance. It is the habit of these ants to retire to the formicary as soon as the sun becomes uncomfortably hot. When this happens the mimic hides itself under the débris. Towards evening the ants again emerge, and the mimic comes out from its hiding-place to join them.

In this instance also the mimic devours the ants with which

it lives. It dare not attack a vigorous harvester, but it wanders about in the vicinity of the nest waiting for a weak or injured worker. Probably it gets a favourable chance when the ants are torpid during cold weather or when they collect in sluggish groups before retiring to the formicary at night. A spring takes place and the harvester is killed instantly. The capture is then carried to some sheltered spot and its juices sucked out at leisure.

The peculiar thing is that the ants are aware of this dangerous associate yet permit it to remain amongst them. They clearly regard it as an enemy. Single workers repeatedly rush at it, but they never make a combined attack. They will fall on the

Text-figure 5.

Ant. *Messor barbarus* Linn.Spider. *Zodariion* sp.

spider if they find it helpless, but otherwise they submit to its presence. Yet harvesters are not lacking in offensive powers, for they frequently combine to drive out other intruders.

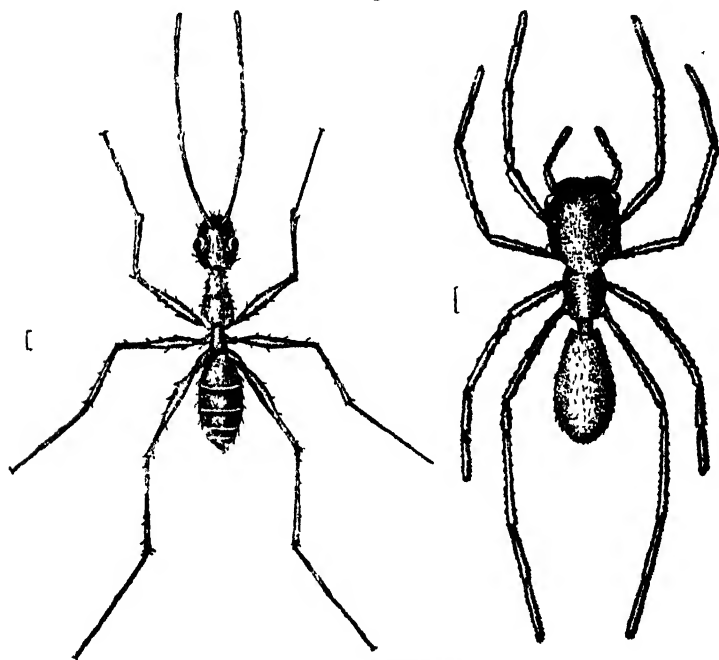
The ants which harbour spider-mimics are usually of a particularly formidable nature. *Camponotus compressus* is very pugnacious and has exceptionally strong jaws. *Ecophylla smaragdina* is notoriously virulent and attacks an intruder in large swarms. *Sima rufo-nigra*, the red and black tree-ant, is fearless, pugnacious, and has a powerful sting. These three species are probably the most formidable in India, and each is freely mimicked by spiders. This point has been brought forward by Mr. Green and regarded by him as an indication that

the purpose of the mimicry is to give protection. No doubt this is true to a great extent. But it does not apply to this mimic of the harvesters. For *Messor barbarus* is an exceptionally peaceful ant. Its daily business is to carry seeds, and it has no special weapons of offence.

Observed at Fyzabad in Central India.

Prenolepis longicornis is a small black ant that commonly frequents bungalows in India. Its mimic is very difficult to detect, so completely is it lost in the *Prenolepis* swarm.

Text-figure 6.



Ant. *Prenolepis longicornis* Lutr.

Spider. *Myrmarachne* sp.

The mimic is a species of *Myrmarachne*. When magnified as shown in the illustration, it does not look very like its model. The magnification is shown by the line on the left. Both are about the same size; both are constricted in the middle, and have long raking legs; both are of much the same tint of colour, though the spider is a little darker than the ant. The chief point of difference is in the head, for the head of the mimic is square and bulky and many times larger than that of its model.

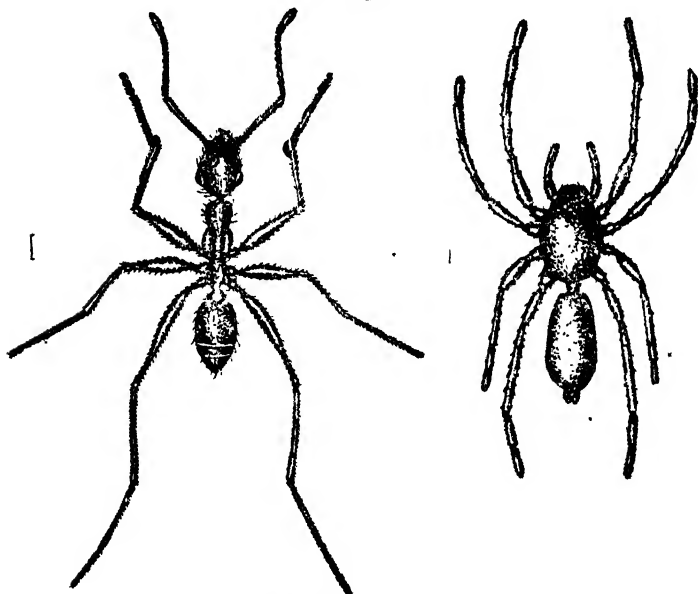
Though not very like when examined minutely, yet the move-

ments of the mimic are so very ant-like that it passes unnoticed in the midst of the swarm. I have never seen it except in company with its model, usually on walls or foliage or on the trunks of trees. It is exceptionally shy and agile, appearing for an instant, then darting off in alarm and being lost in the confusion of ants. The resemblance to its model is further increased by its possessing the habit of thrusting forward its front legs and making them look like ant's antennæ.

Observed at Fyzabad in Central India.

When examined minutely we see no resemblance between *Aphenogaster beccarii* and the *Micaria*. The mimic is somewhat smaller than its model. In each the scheme of colour is identical; head and thorax dark red-brown, legs distinctly paler, abdomen glossy black.

Text-figure 7.



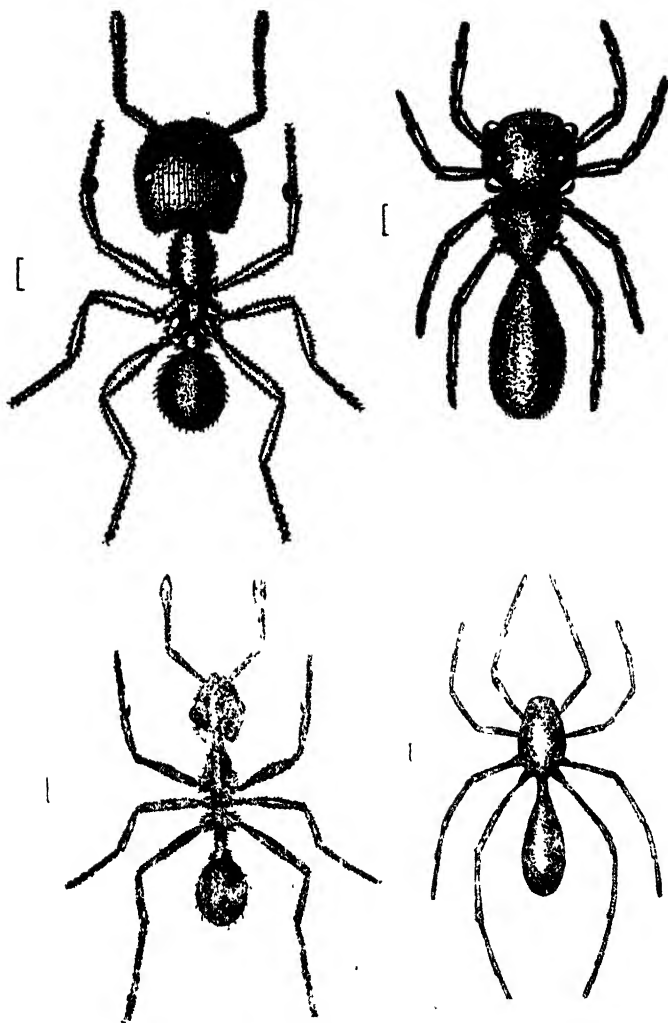
Ant. *Aphenogaster beccarii* Emery.
Spider. *Micaria* sp.

Nevertheless, as in the previous example, the spider is very difficult to detect. Its actions and movements are so exactly ant-like that the absence of anatomical resemblance is of much less importance than one might expect. This mimicry in habit rather than in structure was noticed by Burchell many years ago. Pocock regards it of special interest as suggesting that an imitation of ant-movement may have been the first step of survival value toward the production of a perfect mimic,

Observed at Fyzabad in Central India.

Phidola indica lives in large communities. It nests on the ground and sends out armies which bring dead insects to the nest.

Text-figures 8 & 9.



Ant. *Phidole indica* Mayr.

Spider. *Myrmarachne* sp. and *Mircariolepis* sp.

The workers are of two distinct castes, the soldiers and the smaller workers. The soldiers are large, with big square heads,

and are comparatively sluggish in their movements. The smaller workers are slender and more agile, and are many times more numerous than the soldiers.

The most interesting point in this example of mimicry is that two completely different spiders mimic the separate castes of the ant. The mimic of the smaller caste is a new species of *Micariolepis* (text-fig. 9). Like its model it is slender with attenuated legs. The colours of both are exactly similar; head and thorax reddish yellow, legs pale yellow, abdomen much darker and almost black. Its movements, too, are of the small worker type, that is, much more agile and energetic than those of the soldier caste. Only with the greatest difficulty can it be detected in the midst of the swarm.

The mimic of the soldier is a species of *Myrmarachne* (text-fig. 8). It is a larger and stouter spider, and about the same size as its more bulky model. Its head is square-shaped like that of the soldier; it is markedly constricted between the thorax and abdomen; its legs are much shorter than those of the *Micariolepis* mimic, as are the legs of the soldier shorter than those of the smaller caste. We also see an identity in coloration; head and thorax reddish, abdomen distinctly darker, pale yellow legs. Its behaviour corresponds with that of its model. The soldiers are slow and heavy compared with the movements of the smaller workers. So does *Myrmarachne* move slowly and with hesitation, making turns alternately to one side and to the other, a peculiar mode of progression characteristic of the soldier caste. This side-to-side movement is very distinctive. Peckham noticed it in mimics of the family Salticidæ, and states that, like the ants, they zigzag from side to side and hold up the second pair of legs so as to simulate the ant's antennæ. Also that when feeding they keep up a twitching of the abdomen, pulling their prey about in different directions, beating it with their fore legs, and thus simulating exactly the restless movements of the ants.

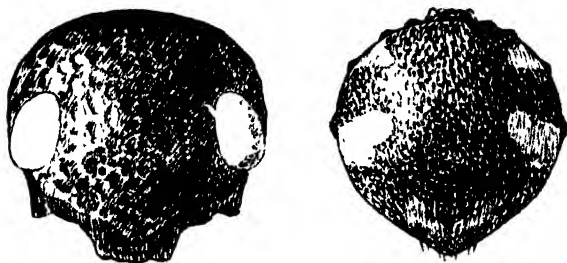
Observed at Jhansi in Central India.

A particularly interesting example of mimicry was observed at the nest of *Phidole indica* Mayr. One evening in January, while the ants were excavating, I noticed two small black spiders running about on the ejected debris. They were very agile, rather globular in shape, and, except for their black colour, did not much resemble the ants. I am informed by M. Fage that they belong to the genus *Dipæna* and are probably a new species.

As I watched the spiders I noticed that, when they became alarmed, they remained motionless, bent down their heads, curled their legs under their bodies, until the only part visible was the black pear-shaped abdomen. The purpose of this behaviour was evident immediately, for scattered about on the ejected debris, as is usually the case with this species of ant, were numbers of ants' heads. These were the decapitated remains of victims. For

this ant drags workers of other species to its nest and throws the heads out on the refuse heap. When the spider curled itself and remained motionless it looked exactly like one of these heads. By ordinary inspection one could not tell which was the spider and which the head. The spider was the same black colour as the head, and similar in size and shape. Moreover, when examined carefully, the spider's abdomen showed on either side a light-coloured oval patch. This corresponds with the eyes on the head which are bleached white on the empty shell. If the antennæ were still attached to the head then, of course, the resemblance would fail, but in the case of these ejected heads the antennæ have always fallen off.

Text-figure 10.



Ant's head.

Spider. *Dipana* sp.

I have little doubt that the purpose of this resemblance was to enable the mimic to live with the ants and give it opportunities to capture them. These mimics appear to be very rare. I carefully examined hundreds of nests, but met with them only on this one occasion.

This example of mimicry is particularly instructive. The spider does not mimic the ants with which it lives, but rather a special fragment of their ejected debris which is common and conspicuous around their nests. This would seem to dispose of the theory which attempts to explain the resemblance between mimics and models by their being exposed to similar conditions in the environment of an ant's nest. Such an explanation could not hold when the spider mimics not the ant but something which the ant habitually casts out.

The Purpose of Ant Mimicry in Spiders.

Some of the most perfect examples of mimicry are found in the resemblances between spiders and ants. Black and white sketches do not properly show it. It is the patches of white hair or the silvery pubescence or the detailed similarity in scheme of colour that make it so very striking in the field.

The resemblance may be of value to the spider in two ways. It may be protective or it may be aggressive, or it may be both.

First, with respect to its protective value. Ants are dominant insects, and have comparatively few enemies. In the tropics they abound everywhere, often congregating in exposed places, yet we seldom see them attacked. Moreover, they are aggressive and well armed, and often combine to make fierce assaults. No doubt a list of the enemies of ants could be prepared. But these would be only occasional depredations. One sometimes sees them falling into the pits of ant-lions, different species attack one another. I have found them in the stomachs of different kinds of birds. But, on the whole, they suffer very little persecution. One has only to watch a swarm of termites emerge and to see how they are decimated by scores of enemies in order to realise how great is the immunity enjoyed by almost all species of ants.

Spiders, on the other hand, are persistently preyed on. By far their chief enemies are hymenoptera and diptera. Digger wasps and mason wasps hunt them relentlessly, pursuing them under leaves and broken bark, or driving them from tunnels in the ground. In the tropics myriads are captured in this way and carried off to provision-cells. In India, Mr. Field counted ninety-eight spiders in a single cell of *Sceliphron cormandelicum*. The Peckhams, referring to this wasp-persecution, express wonder that any spiders are left, "such thousands and tens of thousands are destroyed by these tremendously energetic enemies." We can best appreciate this destruction by recalling their defences, such as dropping from their webs, simulating death, harmonization with inanimate objects, and especially the construction of special devices such as pellets, bands, spirals, zigzags with which they blend when seated in their snares. Other enemies are parasitic diptera which Bristowe saw picking spiders from their webs. Insectivorous birds must destroy them in numbers. I have found them in the stomachs of sun-birds and wall-creepers. But I fully agree with Pocock's conclusion, that wasps are by far their most serious enemies, and that "wasp-persecution has had perhaps a greater effect in moulding and developing the structure and protective instincts in spiders than any other factor in organic nature."

Wasps, on the other hand, rarely attack ants. In fact, they show particular aversion to those insects. The Peckhams have seen the approach of an ant throw a *Pompilus* into a perfect panic. I once placed an ant in the cell of *Rhynchium nitidulum* with the result that the wasp was thrown into a frenzy as soon as it discovered the nature of the intruder. This being so, it is reasonable to conclude that the mimicry has a protective value, the protection being mainly from parasitic wasps.

Has the mimicry an aggressive function? The observations in this paper support this view. Some mimics seem to feed habitually on their models. They have to do so with care and circumspection. The mimic of *Ecophylla* is particularly adept.

It puts itself into an alluring attitude which attracts the attention of its model and gives the mimic an opportunity to spring.

Thus the mimicry would seem to serve a double purpose. It is protective in that it shields the spiders from *Hymenoptera*, aggressive in assisting them to capture prey. This type of mimicry may therefore be regarded as a "combined protective and aggressive resemblance."

How has the mimicry been brought about? Professor Poulton in his 'Essays on Evolution' has discussed this problem in all its details. He rejects the theory of external causes which holds that the likeness between mimic and model can be explained by their living in the same environment. The example of the spider mimicking the ant's head supports the rejection of this simple theory. For in this case the likeness is not to the ant, but to a rejected fragment of its prey. Similarity of environment could not possibly have brought about mimetic resemblance in such a case.

Natural selection is the only theory that supplies a complete and satisfactory explanation. Professor Poulton has expressed himself so clearly on this point that I quote in full the following paragraph from his paper on "The Cause of Mimetic Resemblance" in vol. xxvi. of the Journal of the Linnean Society:—

"When one insect resembles an ant by the superficial alteration of its whole body-form, another by the modification of a shield-like structure which conceals its unaltered body, another by having the shape of an ant painted, as it were, in black pigment on its body while all other parts are concealed; another by a further modification of its body, so that it represents not an ant only, but the object which the ant is almost always carrying,—when the effect of all these results is heightened by appropriate habits and movements, we are compelled to believe that there is something advantageous in the resemblance to the ant, and that Natural Selection has been at work. The phenomena do not merely disprove all other suggested causes of change, but they constitute the most powerful indirect proof of the operation of Natural Selection."

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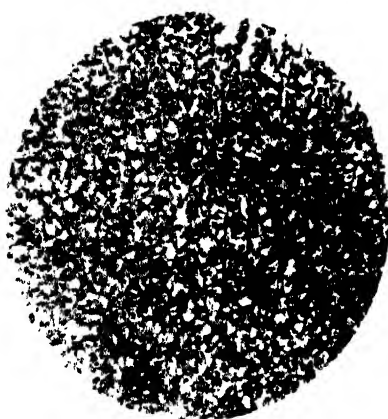
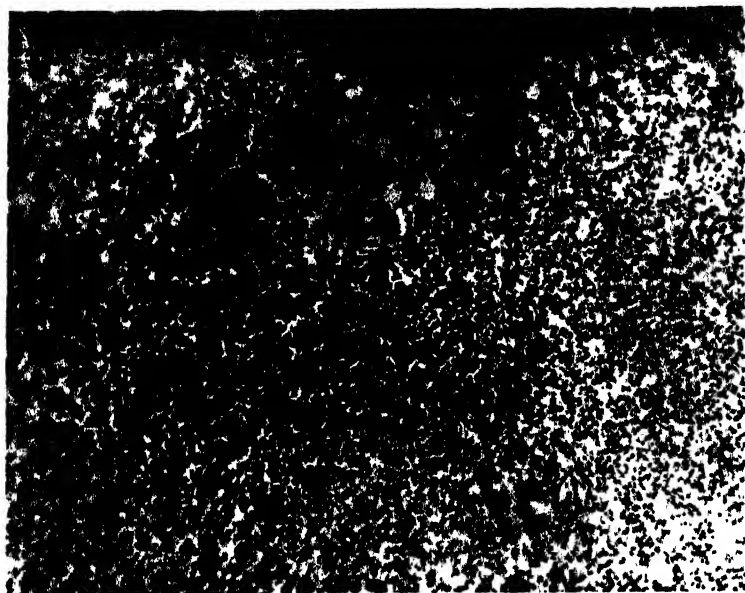


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DOUBLE MALIGNANT TUMOUR OF THYROID AND PARATHYROID
IN AN OTTER (*LUTRA LUTRA*).



4



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DOUBLE MALIGNANT TUMOUR OF THYROID AND PARATHYROID
IN AN OTTER (*LUTRA LUTRA*).

43. Double Malignant Tumour of Thyroid and Parathyroid.

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(Plates I.-II.*)

The neoplasm about to be described occurred in an Otter—*Lutra lutra*—from Norfolk, which arrived in the Gardens on March 21st, 1925. Early in the following year a swelling in the throat was noticed to the right of the mid-line, but the general health of the animal appeared to be good. During April this swelling exhibited a fairly rapid increase in size, and by this time had become a large tumour occupying the middle and right side of the neck. On May 24th, 1926, death occurred suddenly with symptoms of asphyxia.

At the autopsy, performed very soon afterwards, a large swelling was found situated in the mid-line of the throat and the right side of the neck in front. The right lobe of the thyroid was enlarged and occupied by a growth which measured $11.5 \times 6.5 \times 3$ cm., infiltrating the planes of the muscles of the neck laterally, and terminating below in an abscess cavity with necrotic walls (Pl. I. fig. 1). This abscess contained fully half-a-pint of creamy, blood-tinged pus and had involved also the muscles externally and, together with the neoplastic mass, had thrust the trachea well to the left of the middle line. Section of the "thyroid" part of the swelling shows a few breaking down foci, and internal to it, partly overlapped by it and partly wrapped in it, is a paler swelling the size of a small walnut.

For microscopical examination pieces of tissue were taken from the "thyroid" portion anteriorly, posteriorly, and laterally where the muscles were being infiltrated; also from the internal paler tumour.

As regards the other organs and tissues, with the exception of swelling and hardness of the glands in each side of the neck, a little pulmonary congestion and emphysema, everything appeared to be normal. There were no secondary deposits found anywhere.

MICROSCOPICAL STRUCTURE.

All the sections of portions of tissue taken from various parts of the main "thyroid" part of the tumour showed the same

* For explanation of the Plates see p. 864.

structure, and one description will, therefore, suffice. The whole is constituted almost solely of enormous numbers of small round cells, closely packed in most situations, somewhat more loosely in others, resembling small lymphocytes with a very narrow rim of cytoplasm. These infiltrate the capsule and invade the adjacent muscles (Pl. I. fig. 2). The stroma is exceedingly scanty in amount except that the cells are more loosely disposed where an intercellular fibrillar stroma is evident, and near the capsule where trabeculae of fibrous tissue are seen to pass in.

Interspersed among the small cells, but relatively few in number, are other cells some four times the diameter of these; they have a faintly discernible nucleus and a weakly-staining cytoplasm. Several of the small cells contain two nuclei, but the structure of the nucleus in every case is very dense and none shows any definite mitotic figures.

In those places where the cells are more loosely disposed the spaces so produced have no proper lining; they appear to be mere rifts, as it were, in the cellular mass. Small hæmorrhagic extravasations are scattered throughout. Nowhere, in any of the sections, is any colloid visible, nor, in fact, any structure resembling ordinary thyroid tissue.

A portion taken from the swollen part of the left thyroid shows marked infiltration of the stroma with small round cells, but much more loosely arranged than in the right. The characters of the cells are identical in the two cases, but whereas on the right side everything almost is obliterated by the tumour cells, in the left the cells are in focal deposits with unaffected or little affected areas intervening.

Close search through several sections made from different portions of the thyroid tumour fails to reveal any indication of an alveolar disposition of the cells. The importance of this fact will be demonstrated later.

The inner tumour shows at its periphery the general structure resembling parathyroid tissue, glandular cells disposed in rays and columns (Pl. II. fig. 4), but in most parts of the growth the cells are irregularly arranged, are interspersed with hæmorrhagic extravasations, and several exhibit mitosis. The connective tissue of the outer parts passes from the parallel disposition to an irregular one, and in certain situations there are areas or foci of cells separated from the surrounding tissue by a thin fibrous strand like a capsule, which, however, is not as a rule complete.

There are elsewhere small scattered foci of a dozen cells or so among which are numerous small extravasations of blood; these cells are of a squamous appearance or large cells like those of the parathyroid, and often show mitosis (Pl. II. fig. 5).

We have, therefore, an instance of a rare condition: the presence of two malignant growths in the same animal, namely, a small round-cell sarcoma of the thyroid and a carcinoma of the parathyroid.

I can find no record in the literature at my disposal of

malignant growth of the parathyroid occurring in the human subject. In veterinary literature, as quoted by Ball, there are three cases mentioned. The first was found by Professor Petit in a dog. In this, both "thyroids" were hypertrophied, and on cutting open were found to contain abnormal nodular formation. Metastases were present in the lungs, the pericardium, the kidneys, and suprarenals. Histologically it is described as a "double epithelioma of the deep parathyroids," constituted by rays of epithelial cells with large nuclei, identical with cells of the parathyroid, and with a condition of telangiectasis. The metastases had the same "parathyroid" structure.

The same author also mentions two cases occurring in the horse—"the structure in one was that of embryonic parathyroid," he states, "in the second that of adult parathyroid."

Multiple neoplasms, particularly of benign forms, such, for instance, as fibromyomata, are not uncommon; but two or more quite different neoplasms occurring in the same individual, though well authenticated, are nevertheless sufficiently uncommon to merit being placed on record.

It is well known from experimental work on cancer that the presence of a primary malignant tumour has an inhibiting effect on the subsequent development of a second, not, of course, of metastatic deposits from the first, but of a distinct primary new growth. Two primary carcinomata declaring themselves at about the same time from simultaneous irritation or even irritation at an interval, provided that this is not long enough to allow a primary tumour to develop, has been repeatedly demonstrated. Refractoriness appears to arise only when irritation is attempted after the first carcinoma has declared itself. These remarks and findings apply to carcinomata. The rarity of simultaneous carcinoma and sarcoma as independent tumours is even greater, perhaps because the latter, in Man at least, occurs at an early age, whereas the former is a disease of more advanced life.

Two important questions present themselves when we meet with conditions such as those described in the case of this Otter. Firstly, are we dealing with a sarcomatous transformation of stroma, the stimulus of a carcinomatous growth leading to malignant stimulation of the stroma of the epithelial tumour itself, such as is seen occasionally in certain mouse-carcinoma? Secondly, are we dealing with a sarcoma at all, or merely with a polymorphic development in a carcinoma?

A carcinoma of the breast in a mouse has on several occasions been recorded as setting up such activity in the stroma as to produce a true sarcoma, and the growth of the latter was so rapid as to obscure that of the primary carcinoma.

The fact that the internal tumour in our case was a parathyroid carcinoma and that adenoma of the parathyroid may occur within or closely adjacent to the thyroid might lend support to this view, but such tumours have clearly the structure of the parathyroid,

whereas in the Otter the inner tumour is seen to be quite distinct macroscopically from the outer, and in the latter, microscopically, there is no trace whatever seen of any parathyroid tissue.

Primary malignant growths of the thyroid are both uncommon, but of the two sarcoma is probably the more so, whereas carcinoma not infrequently develops in goitrous enlargements of the gland—according to Professor Bérard as high a proportion as 80 per cent. Sarcoma of the thyroid is rather more frequently of the spindle-cell type, or may be found as angiosarcoma or osteochondrosarcoma or as a member of that debatable class, endothelioma. In this instance it was of the small round-cell type, the most malignant of the malignant connective-tissue growths, and in the case of the thyroid they are prone to early invasion and compression of surrounding structures.

In Man, carcinomata of the thyroid vary considerably in their grade of malignancy: whereas some extend rapidly and give rise to metastases early, others are of slower growth and do not disseminate till late. Whereas many contain colloid, not only in the primary tumour, but also in the metastases, some are composed almost entirely of cells without any demonstrable colloid, and their origin from the thyroid is determined by macroscopic appearances.

In veterinary pathology there is considerable divergence of opinion on the subject of malignant disease of the thyroid. On the one side Fodéré, Scarpa, Kostum, and others maintain that all thyroid cancers are secondary to disease elsewhere; Duplay holds an intermediate position, namely, that primary carcinoma is as rare as secondary is frequent; Houel affirms, on the contrary, that most of them are primary and that secondary are exceptions. There is no doubt, however, that, on the whole, such tumours are met with comparatively often, and especially in the dog, the cat, and the horse, and in wild animals we have seen them in raccoons, jackals, and genets.

If the growth is a diffused one the general contour of the gland is retained, but most are nodular; hæmorrhage into the growth is common, as is also cyst-development. The microscopic structure of malignant tumours of the thyroid varies considerably; we may see a typical adenocarcinoma, or an acinous papillary form, or a branchogenic epithelioma, a heterotopic squamous epithelioma originating in branchial inclusions, or finally, osteoid carcinoma, as seen sometimes in Man. Amongst domesticated animals all these are commonest in the dog.

As regards sarcomatous involvement of the thyroid in wild animals, Herbert Fox records three cases in his well-known work on 'Disease in Captive Wild Mammals and Birds' (pp. 333-5). The first of these was a Raccoon-like Dog (*Canis procyonoides*) in which the tumour is diagnosed as adenocarcinoma sarcomatodes with metastases in the liver and lungs. The following is an abstract of his report:—

At the level of the thyroid on each side is a rounded encapsulated nodule, $2.5 \times 2 \times 1$ cm.; parts are hard, parts show foci of cystic softening; below these are the bodies of the thyroid, $5 \times 2.5 \times 2.5$ cm., firm but containing cystic foci.

Histologically the thyroid shows a firm dense capsule of irregular thickness, seemingly owing to penetration of enclosed tumour cells; the inner limit of the capsule is therefore irregular and at times thinned till it is reduced to nil. Appearances within the capsule vary; in places they are those of carcinoma, but as regards the connective tissue, there are (a) areas of closely-packed large spindle-cells with hyperchromatic nuclei, having no regular relation to the epithelial elements, (b) in other parts similar spindle-cells, but arranged to form irregular capillaries; and (c) a combination of the other two; acini, some of which contain colloid, are present, and between them run blood-capillaries with rich and numerous embryonic lining cells.

The second case was a Prairie Wolf (*Canis latrans*) with a mixed tumour of the thyroid and metastasis in the lungs. The gland was the size of a child's head; it was firm, and 300 c.c. of blood-stained fluid was obtained from it; the remainder was soft and friable as if made up of fatty and hæmorrhagic matter. Histologically the gland was largely sarcomatous, with a round-cell alveolar arrangement dominant at one place, at another short spindle-cells; many areas of small and a few of large hæmorrhage. Section of the lung showed a large sarcoma nodule (round cells).

The third was a Coypu (*Myocaster coypu*). The upper part of the right lobe of the thyroid was occupied by, or at least within the same capsule as, a pink mass, $25 \times 15 \times 10$ mm. It was soft, mushy on section, with very delicate trabecular network.

Histologically the mass was almost completely cellular with here and there delicate and incomplete trabeculations. Small blood-vessels were numerous—a delicate line with a cell-nucleus here and there—no true wall, but, as it were, spaces as blood-channels through the cell-mass. Here and there were compressed remains of thyroid acini. The cells were irregular in shape and size, with nucleus usually eccentric.

The question of mixed tumours of the thyroid is a much debated one and every case calls for most careful examination and cautious interpretation. There is, undoubtedly, much polymorphism in thyroid carcinomata, not merely an admixture of solid and acinous structure, but such extreme polymorphism of cells that they may lose the characters of epithelium and resemble very strongly connective-tissue cells. The so-called carcinosarcomata are "essentially carcinomata in which the stroma has sarcomatous properties" (*Kettle*). Some of the instances denominated carcinosarcomata are merely examples of this polymorphism, so that the alveolar type may pass to the "solid alveolar" or trabecular type, and the latter to loose sarcomatous type. Further, if a thyroid tumour is growing rapidly, as the effect of compression, the alveolar character is lost and the cells come to resemble very markedly those of sarcoma.

Besides such polymorphism there may be a diffuse lymphocytic infiltration in a rapidly growing carcinoma; this is seen in some tumours of the breast. Though this infiltration may lead on cursory examination to the diagnosis of carcinosarcoma, it will be noted that the infiltration is not separate from but intimately interspersed amongst the cancer tissue.

Ewing is very definite regarding the doubtfulness of sarcoma of the thyroid. Transformation of the thyroid *epithelium* is, he maintains, so fully established that the occurrence of true sarcoma in Man has still to be demonstrated. He certainly adduces some cogent evidence in support of his contention.

Carcinoma and [so-called] sarcoma are found at about the same age, the chief difference clinically being the more rapid course of the latter. Macroscopically they are similar—large tumours, circumscribed or diffuse, invading adjacent tissues and producing metastases. Morf's analysis of 40 cases gives 10 as round cell in type.

The fact that close histological examination in many of the recorded cases revealed an alveolar structure favours epithelial origin, while the figures depicted in Wolfer's alveolar sarcoma of the thyroid are (according to Ewing) indistinguishable from what is seen in some forms of carcinoma, and Kaufmann's case, diagnosed after careful study, as a round-celled sarcoma showed a distinctly alveolar disposition of cells.

Aschoff, however, states that tumours of mingled carcinomatous and sarcomatous characters do occur in the thyroid and, moreover, that metastases may be of one or other kind.

In the case of the Otter, the subject of this paper, detailed examination of various pieces from the thyroid portions of the tumour fails to reveal any alveolar arrangement of the cells; they are of the small round-cell type almost entirely, and they invade the surrounding structures; there was no concomitant carcinoma of the thyroid, this form of neoplasm being found in the parathyroid as an adenocarcinoma.

Death was the result of compression due in part to the mass of the growth, in part to the large abscess and necrotic lower portion of it, and in part to dislocation of the trachea, before any recognizable metastases had time to develop.

I wish to express my acknowledgments to Mr. F. H. Bond and Mr. F. Martin Duncan, F.R.M.S., F.Z.S., to the former for the photograph for Fig. 1, and to the latter for Figs. 2-5.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. Photograph of the tumour in the right side of the neck of an Otter (*Lutra lutra*), showing enlargement of the thyroid and parathyroid glands. The lower part was converted into a large abscess containing pus, blood, and necrotic tissue. The trachea is thrust to the left of the mid-line.

Fig. 2. Section of the outer part of the thyroid portion of the tumour, showing a small round-cell sarcoma invading the muscle-planes on the left of the section. Low power.

PLATE II.

Fig. 3. A small portion of the last, under higher magnification, showing the growth to be composed almost entirely of small round cells. No recognizable thyroid tissue remains.

Fig. 4. Section of the parathyroid portion of the tumour, showing in the upper part the trabecular arrangement of the glandular epithelial cells, becoming irregular in distribution to the right and below.

Fig. 5. Portion of the last under higher magnification, showing the irregular distribution of the cells, penetrating in all directions. Many of the nuclei exhibited mitotic figures.

44. Contributions to the Development of the Pelvic Girdle :
II.—The Pelvic Girdle in the Batrachian *Hynobius nebulosus* s. *Ellinoglossa nebulosa* Dum. et Bibr. By JAMES W. LOW, B.Sc., F.Z.S., Department of Zoology, University of Bristol.

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(Text-figures 1-5.)

In this paper a description is given of a number of stages in the development of the pelvic girdle of *Hynobius*. The material consisted of six embryos, 16·5 mm., 17-18 mm., 19·5 mm., 25 mm., 28 mm., and 33 mm. respectively. Transverse sections were cut of the hinder portions of these and reconstructions of the pelvic girdles made by the wax-plate method. In the case of the 25 and 33 mm. embryos, the pelvic muscles were reconstructed and also the nerves in the older stage. I have been unable to find any description of the pelvic musculature in the adult, but the adult condition has practically been reached in the 33 mm. embryo. This was confirmed by dissection of the pelvic muscles in an adult specimen.

I desire to express my thanks to Professor F. H. Edgeworth for his kindness in giving me the material.

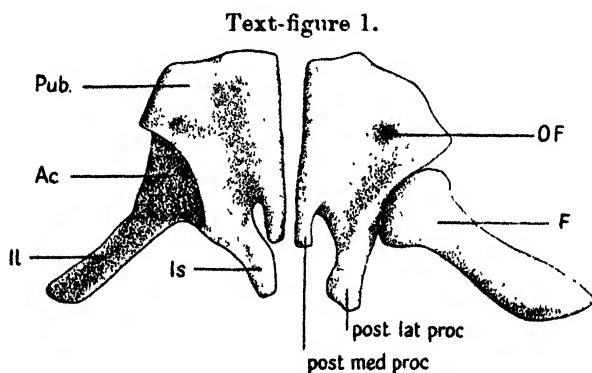
THE PELVIC GIRDLE IN THE YOUNGER EMBRYOS.

Examination of three stages between 16·5 and 19·5 mm. in length shows that the hind limb arises as a bud in the posterior region of the body immediately in front of the cloacal aperture, when the myotomes of the dorsal part of the body are already well developed and clearly differentiated in their histological appearance. The first trace of the hind limb (16·5 mm. stage) is a distention of the ectoderm by an undifferentiated mass of mesenchyme ventro-laterally, on each side of the coelom and not separated from the coelomic epithelium. Soon, however, the anlage of each limb becomes a distinct papilla projecting from the body. This continues to grow outwards and backwards, the cells inside becoming gradually separated into masses, which will give rise to the femur and the pubo-ischial portion of the girdle. A nerve passes down into the limb-bud and bifurcates into a dorsal and ventral branch. In the most advanced of the three stages no definite muscular tissue or cartilage is as yet formed in the limb-buds.

THE PELVIC GIRDLE IN THE 25 MM. EMBRYO. (Text-fig. 1.)

The pelvic girdle at this stage consists of two distinct halves, each of which is composed of a ventral portion and a process directed upward and backwards. These two cartilages are inclined to one another at an angle of about 110° , forming a wide V-shaped structure.

Each half consists of a continuous mass of cartilage which can be considered, for purposes of description, as consisting of a dorsal iliac region, an antero-ventral pubic region, and a postero-ventral ischial region, meeting in the acetabular region, but there is nothing to indicate the exact limits of the respective regions. Each cartilage bears on its outer side,



Drawing of modal ($\times 100$) of pelvic girdle of 25 mm. embryo.

Ventral aspect, scale $\frac{1}{2}$ approx.

at about the middle of its length and below the point of origin of the iliac process, a shallow depression, the acetabulum, with which the femur articulates.

Fossa acetabuli:

The acetabulum consists of a shallow depression, facing ventro-laterally, on the outer side of each cartilaginous mass. It is marked off anteriorly from the pubic region by a prominent ridge. It is bounded posteriorly by a slight ridge, while dorsally the acetabular surface is continuous with the outer surface of the ilium.

Regio iliaca:

The iliac portion of the cartilage consists of a somewhat flattened prong-like process arising dorsally to the acetabulum and projecting obliquely upwards, backwards, and outwards. This iliac process is elliptical in section, the inner surface passing anteriorly into the dorsal surface of the pubo-ischium.

The outer surface curves gradually at its lower end into the acetabular surface. The anterior border is rounded, and slopes downwards from the free end to the dorso-lateral margin of the pubic region. The posterior border is rounded, and slopes downward and forward from the free end, bounding the ilio-ischiadic notch dorsally.

Regio ischiadica :

The ischial region consists of a mass of cartilage, fairly broad anteriorly in the acetabular region and continuous with the pubic region; posteriorly it is produced into two processes, medial and lateral respectively. The postero-medial process is about half the length of the postero-lateral process, is somewhat oval in section, and forms a backward continuation of the median border of the pubo-ischium. The postero-lateral process arises behind the acetabulum and projects backwards and slightly inwards, somewhat above the level of the medial process, from which it is separated by a deep notch.

The acetabular portion is somewhat triangular in section. Its dorsal surface is smooth, and is continuous anteriorly with the dorsal surface of the pubic region. The ventral surface is concave, a wide groove passing to the notch separating the posterior processes. The ventro-lateral border bounds the acetabulum below and terminates in a slight ridge behind the acetabulum, separating it from the postero-lateral process. The ventro-medial border is rounded and continuous with the corresponding border of the pubic region.

Regio pubica :

The pubic region consists of a mass of cartilage lying in front of the acetabulum. It is somewhat triangular in transverse section, the apex directed upwards. The dorsal surface is smooth, and is continuous behind with the dorsal surface of the ischial and iliac regions. The ventral surface, perforated somewhat laterally by a small obturator foramen, is continuous with the ventral surface of the ischial region. The obturator foramen lies at the front end of the groove, which slopes towards the notch between the postero-lateral and postero-medial processes of the ischial region. The lateral surface may be considered as consisting of two aspects, an acetabular face and a pre-acetabular face, separated by a prominent ridge bounding the acetabulum anteriorly. The acetabular face slopes downwards from the dorso-lateral margin of the acetabulum, forming part of the acetabular surface. The pre-acetabular face is a somewhat concave triangular area, facing antero-dorsally, lying between the dorso-lateral and ventro-lateral margins. The obturator foramen lies in the concavity. The ventro-lateral margin, which forms an elbow at the lower end of the ridge bounding the acetabulum, slopes inward and forward

projects forwards as a blunt process, separated from the antero-medial process by a wide shallow notch. The pre-acetabular aspect faces more anteriorly, and the elbow in the ventral-lateral margin, in front of the acetabulum, has become less prominent.

THE PELVIC GIRDLE IN THE 33 MM. EMBRYO. (Text-figs. 3 & 4.)

There is only a relatively small increase in the length and breadth of the girdle as compared with the 28 mm. stage. The cartilages are much thicker, and the adjacent medial borders are still more closely approximated in the mid-ventral line. At the anterior end a fusion of the antero-medial processes of the earlier stage has taken place, forming a median cylindrical process which passes forward into the ypsiloid procartilage.

Fossa acetabuli :

The acetabulum has become deeper, and is still more clearly demarcated from the surrounding regions. The ridge anterior to the acetabulum is much more prominent, and the elbow at its lower end obliterated by the growth of the cartilage. Dorsally there is a more prominent ridge separating the acetabular surface from the outer surface of the iliac region. The post-acetabular notch still remains.

Regio iliaca :

The relationships of this area are essentially as in the 28 mm. stage. The posterior portion is flat and expanded, but now tapers forward to a thin region, oval in transverse section, before merging in the ventral cartilage. The iliac process in this stage is connected by a ligament to a transverse rib attached to the sacral vertebra.

Regio ischiadica :

The vacuities of the 28 mm. stage are becoming obliterated. A fairly large vacuity still remains on the right side only, in line with the posterior margin of the acetabulum. The process bounding the acetabulum posteriorly is more prominent. The ilio-ischiadic notch is much wider and more rectangular in shape. The dorsal surface of the ischial region is slightly concave and continuous anteriorly with the dorsal surface of the pubic region. The ventral surface of the ischial plate is flat, but curves downwards in the acetabular region and is continuous in front with the ventral surface of the pubic region. The lateral and posterior borders are thin and rounded. The medial border becomes thicker as it passes forward, forming, in the acetabular region, a flat face, which is closely approximated to the corresponding face of the cartilage of the opposite side.

Regio pubica :

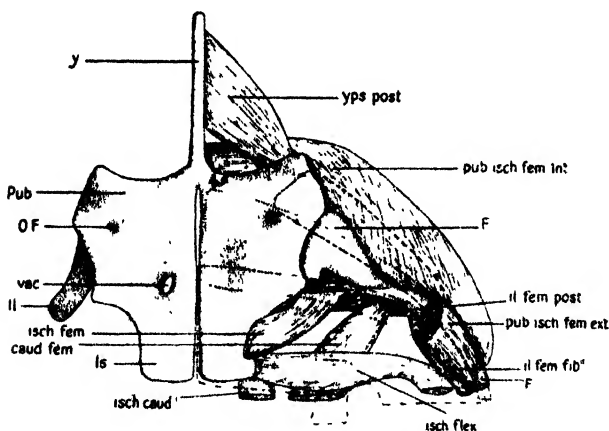
The pubic region is now considerably thickened, especially in the acetabular region, but slopes off abruptly towards the anterior

margin. The antero-dorsal surface slopes down more steeply to the obturator foramen at its base, between it and the small triangular plate formed by the antero-lateral process, which projects forward. The ventral surface is continuous behind with the ventral surface of the ischial region, and is slightly concave from side to side. It slopes gradually forward to the obturator foramen, where the cartilage is thickest in transverse section, and then slopes sharply upwards to the anterior border. The antero-lateral angle forms the small projecting plate referred to above. The antero-medial angles of each side pass gradually into a median procartilaginous process, continuous with the cylindrical ypsiloid procartilage, in the mid-ventral line. It is about two-thirds of the length of the rest of the girdle. The anterior border of the pubic region is rounded and concave from the medial to the antero-lateral process.

THE PELVIC MUSCLES IN THE 33 MM. EMBRYO. (Text-figs. 3 & 4.)

The pelvic muscles were reconstructed in the models of the girdles of the 25 and 33 mm. embryos. The muscles in the

Text-figure 3.



Drawing of model ($\times 100$) of pelvic girdle of 33 mm. embryo.

Ventral aspect, scale $\frac{1}{4}$ approx.

The position of *M. pubo-ischio-tibialis* and *M. caudali-pubo-ischio-tibialis* are indicated by , that of *M. pubo-ischio-femoralis externus* by , and that of *M. pubo-tibialis* by -----.

older embryo, which are practically similar to the conditions found in an adult specimen dissected, are described below. The terminology used is as in a previous paper (1).

(A) The muscles passing backwards from the anterior end of the body which are inserted into the pelvic region are :—

M. rectus abdominis (pubo-thoracicus) :

This consists of two thin narrow bands of muscle lying on either side of, and close to, the linea alba. These are inserted into the anterior margin of the pubic plate. Lying dorsal to this flat muscle is a small muscle which arises from the antero-lateral process of the pubic region and is inserted into the side of the ypsiloid procartilage. This is the *M. ypsiloideus posterior* (3).

M. obliquus externus (costo-abdominalis externus) :

This sheet of muscle is inserted into a ventral aponeurosis, and more posteriorly into the ventral surface of the pubic region in front of the obturator foramen.

(B) The muscles passing forward from the tail which are inserted in the pelvic region are :—

M. ischio-caudalis :

This is a strap-like muscle, lying obliquely to the vertical plane and inserted into the postero-lateral angle of the ischial region.

Innervation : An ischio-caudal branch from the sciatic plexus.

M. caudali-pubo-ischio-tibialis :

This is a small muscle which passes forward ventral to the *M. caudo-femoralis* and is inserted into the posterior edge of the *M. pubo-ischio-tibialis* a short way after the latter muscle has left the ischial region.

Innervation : N. pudendus.

M. caudo-femoralis :

This is a fairly large muscle, somewhat round in section, lying outside the *M. ischio-caudalis* and dorsal to the *M. caudali-pubo-ischio-tibialis*. It tapers somewhat anteriorly, and is inserted into the femur below the trochanter and dorsal to part of the insertion of the *M. pubo-ischio-femoralis externus*.

Innervation : N. pudendus.

(C) The ventral muscles of the thigh are :—

M. pubo-ischio-tibialis :

This is a very large triangular sheet of muscle which arises from an aponeurosis in the mid-ventral line along the hinder two-thirds of the line of approximation of the halves of the pubo-ischium. It covers the hinder portion of the *M. pubo-ischio-femoralis externus* and converges laterally and distally to be inserted into the tibia.

Innervation : N. pubo-ischio-tibialis.

M. pubo-tibialis :

This is a thin strap-like muscle which arises from the ventral surface of the pubic region at the base of the antero-lateral process and behind the insertion of the *M. obliquus externus*. It runs distally, overlapping the margin of the *M. pubo-ischio-tibialis*, to be inserted into the tibia. No muscle is present in this position in *Menopoma* (1).

Innervation : A branch from the N. pubo-ischio-tibialis.

M. ischio-flexorius :

This muscle arises from the postero-lateral angle of the ischial region, just in front of the insertion of the *M. ischio-caudalis* and passes downwards below the knee.

Innervation : A branch from the N. pubo-ischio-tibialis.

M. pubo-ischio-femoralis externus :

This is a thick triangular muscle which arises from the ventral surface of the pubo-ischium very close to the medial border. Its origin reaches from the base of the ypsiloid procartilage anteriorly to a point in line with the hinder limit of the pubo-ischium, and is overlapped behind by the *M. pubo-ischio-tibialis*. It is inserted into the trochanter femoris, just below the insertion of the *M. caudo-femoralis*, and also into the femur below and distal to the origin of the femoro-fibular head of the *M. ilio-femoro-fibularis* down to the tibial condyle.

Innervation : N. obturatorius and a branch from the N. pubo-ischio-tibialis, arising close to the sciatic plexus.

M. ischio-femoralis :

This consists of two intimately associated muscles :—

- (a) A dorsal, more or less cylindrical muscle which arises from the lateral border of the ischial region in front of the origin of the *M. ischio-flexorius* and passes forward to be inserted on the head of the femur ; and
- (β) a smaller ventral muscle which arises from the ventral surface of the ischial region immediately below and closely associated with the origin of α and passes forward to be inserted into the hip-joint capsule.

Innervation : A small branch from the sciatic plexus.

(D) The dorsal muscles of the thigh are :—**M. pubo-ischio-femoralis internus :**

This muscle arises from the middle line along the dorsal surface of the pubic region and, for a short distance, from the dorso-lateral aspects of the antero-median process continuous with the ypsiloid procartilage. It passes over the antero-lateral process, the antero-dorsal aspect of the pubic region,

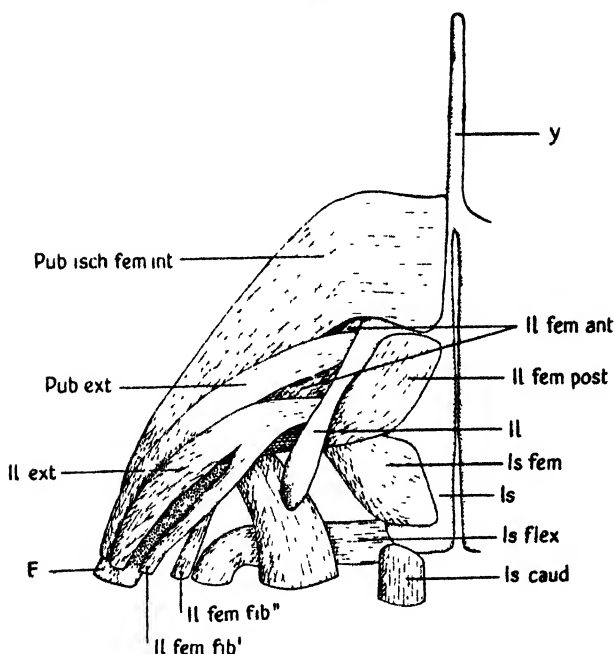
and over the dorsal side of the hip-joint, where it bends at an obtuse angle and passes downwards, expanding over the dorsal side of the femur, into the lower two-thirds of which it is inserted. The origin does not extend back to the ischial region, as does the homologous muscle in *Menopoma* (1).

Innervation: N. femoralis and a twig from the N. obturatorius.

M. pubo-extensorius:

The muscle which corresponds to the muscle so named in *Menopoma* is strap-shaped and arises from the dorso-lateral

Text-figure 4.



Drawing of left half of model ($\times 100$) of pelvic girdle of 33 mm. embryo.
Dorsal aspect, scale $\frac{1}{2}$ approx.

border of the acetabular portion of the pubic (or iliac?) region immediately behind the M. pubo-ischio-femoralis internus, and passes downwards, overlying the posterior edge of that muscle to be inserted in an aponeurosis on the tibial side of the knee.

Innervation: A branch from the N. peroneus.

M. ilio-extensorius:

This is a strap-shaped muscle which arises, along with the ilio-fibular head of the M. ilio-femoro-fibularis, from the outer

surface of the iliac region immediately behind the *M. pubo-extensorius*. The two muscles, which arise from a common origin, soon diverge, the *M. ilio-extensorius* passing downwards to be inserted in the lower leg.

Innervation: *N. femoralis*.

M. ilio-femoro-fibularis:

The ilio-fibular head of this muscle is a long slender strap-like muscle which arises from the outer surface of the iliac region along with the preceding muscle. It passes down to be inserted about the middle of the peroneal side of the fibula. The femoro-fibular head is a slender cylindrical muscle which arises from the femur below and distal to the insertion of the *M. caudo-femoralis* and passes downward beside the ilio-fibular head, becoming closely associated with the latter at its insertion.

Innervation: A branch from the *N. tibialis communis*.

M. ilio-femoralis:

This consists of two intimately associated muscles, *M. ilio-femoralis anterior* and *posterior* respectively, as in *Menopoma*.

The anterior muscle arises from the dorso-lateral margin of the pubic (or iliac?) region immediately below the *M. pubo-extensorius*, by which it is covered. It is inserted into the peroneal side of the femur.

The posterior muscle is larger, and arises as a strap-like muscle from the dorsal surface of the pubo-ischium, passes backwards to the ilio-ischiadic notch, where it bends over the posterior aspect of the ischial region, and then passes distally beside the anterior muscle, near which it is inserted into the femur.

Innervation: *N. peroneus*.

THE PELVIC MUSCLES IN THE 25 MM. STAGE.

Some of the muscles already exhibit the relationships seen in the 33 mm. stage. The differences worthy of note may be briefly summarized.

M. ischio-caudalis passes forward from the tail, but does not yet reach the hind end of the ischium.

M. caudali-pubo-ischio-tibialis is inserted into the hind end of a mass of muscular tissue lying behind the ischium and from which the *MM. ischio-femoralis* α and β , *M. pubo-ischio-tibialis*, and *M. ischio-flexorius* arise.

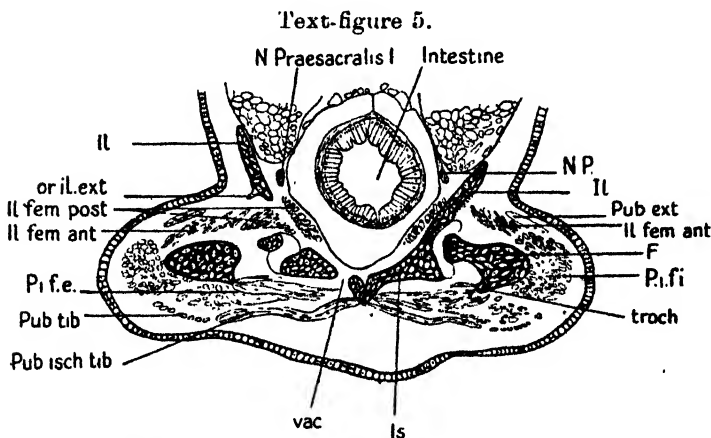
M. pubo-tibialis could not be distinguished from the main mass of ventral muscles, except at some points posteriorly.

M. ischio-flexorius arises from the mass of muscular tissue mentioned above.

M. pubo-ischio-femoralis externus is, at its origin, scarcely distinguishable from the *M. pubo-ischio-tibialis*.

MM. ischio-femoralis α and β arise from the muscle mass behind the ischium.

M. pubo-ischio-femoralis internus arises from the lateral border of the pubic region and passes down over the head of the femur to be inserted as in the 33 mm. stage. The origin does not yet extend to the dorsal surface of the pubic region.



Transverse section (slightly oblique) of 33 mm. embryo, just posterior to the acetabulum.

M. ilio-femoralis posterior arises from the hinder aspect of the ilio-ischiatic notch, and does not pass forward on to the dorsal surface of the girdle as in the later stage.

THE NERVES OF THE PELVIC REGION.

The nerves supplying the pelvic region and the hind limb were reconstructed in the 33 mm. stage. They are derived from three spinal nerves, N. sacralis and NN. præsacrales I. and II. respectively. The terminology used by Osawa (2) is adopted here.

The pelvic nerves form plexi anterior and posterior to the iliac process. The anterior or lumbar plexus is formed by the NN. præsacrales II. and I., a branch from the latter joining the N. præsacralis II. above the acetabulum. This plexus gives off three branches:—

N. obturatorius: This runs forward and inwards, parallel with the dorso-lateral border of the pubic region, towards the obturator foramen. It penetrates the M. pubo-ischio-femoralis internus and passes through the obturator foramen to supply the M. pubo-femoralis externus.

N. femoralis: This passes downwards from the plexus, giving two branches which penetrate the *M. pubo-ischio-femoralis internus*; one of these passes distally close to the inner side of the femur.

A fine branch, which may correspond to the hypogastricus, comes off from the *N. præsacralis II.* before it joins the plexus and passes outwards towards the skin.

The larger posterior or sciatic plexus is formed by the *N. præsacralis I.* and the *N. sacralis*. This plexus lies behind and below the iliac process, above the *M. caudo-femoralis*. Its main branches are:—

N. peroneus: Arises from the outer anterior side of the plexus and passes downwards between the *M. ilio-extensorius* and the *M. ilio-femoralis*.

N. tibialis communis: It arises as two trunks separated by a blood-vessel. They unite at the knee. The collateral trunks are not separated as in *Menopoma* by the *M. caudo-femoralis* nor by the ilio-fibular head of the *M. ilio femoro-fibularis*.

N. pubo-ischio-tibialis: This arises ventrally from the plexus, and passes between the *M. caudo-femoralis* and *M. ischio femoralis* to supply the *M. pubo-ischio-tibialis*.

N. pudendus: Arises from the posterior end of the sciatic plexus and supplies the *M. caudali-pubo-ischio-tibialis*, *M. caudo-femoralis*, and *M. ischio-caudalis*.

A small twig from the sciatic plexus supplies the *M. ischio-femoralis*.

Abbreviations used in Text-figures.

Ac. Acetabulum. *ant.lat.proc.* Antero-lateral process of pubic region. *ant.med. proc.* Antero-median process of pubic region. *caud.fem.* *M. caudo-femoralis*. *F.* Femur. *Il.* Iliac region. *il.fem.ant.* *M. ilio-femoralis anterior*. *il.fem.post.* *M. ilio-femoralis posterior*. *il.ext.* *M. ilio-extensorius*. *il.fem.fib.* Ilio-fibular head of *M. ilio-femoro-fibularis*. *il.fem.fib.* Femoro-fibular head of *M. ilio-femoro-fibularis*. *Is.* Ischial region. *isch.caud.* *M. ischio-caudalis*. *isch.fem.* *M. ischio-femoralis*. *isch.flex.* *M. ischio-flexorius*. *N.P.* *N. pra-sacralis*. *O.F.* obturator foramen. *or.il.ext.* origin of *M. ilio-extensorius*. *post.lat.proc.* Postero-lateral process of ischial region. *post.med.proc.* Postero-median process of ischial region. *Pub.* Pubic region. *pub.ext.* *M. pubo-extensorius*. *pub.tib.* *M. pubo-tibialis*. *pub.isch.fem.ext.(p.i.f.e.).* *M. pubo-ischio-femoralis externus*. *pub.isch.fem.int.(p.i.f.i.).* *M. pubo-ischio-femoralis internus*. *troch.* trochanter femoris. *vac* vacancy in pubo-ischium. *Y.* Ypsiloid procartilage. *yps.post.* *M. ypsiloideus posterior*.

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1. *SCELOTES CAFFER*



2. *SCELOTES BIPES*



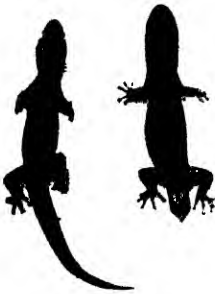
3. *SCELOTES ANGUINA*



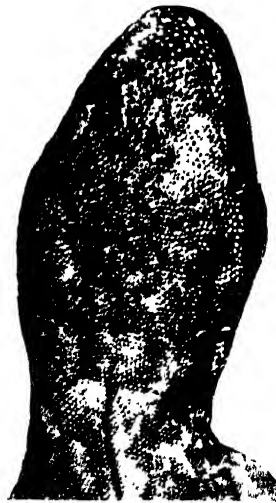
4. *SCELOTES BREVIPES*



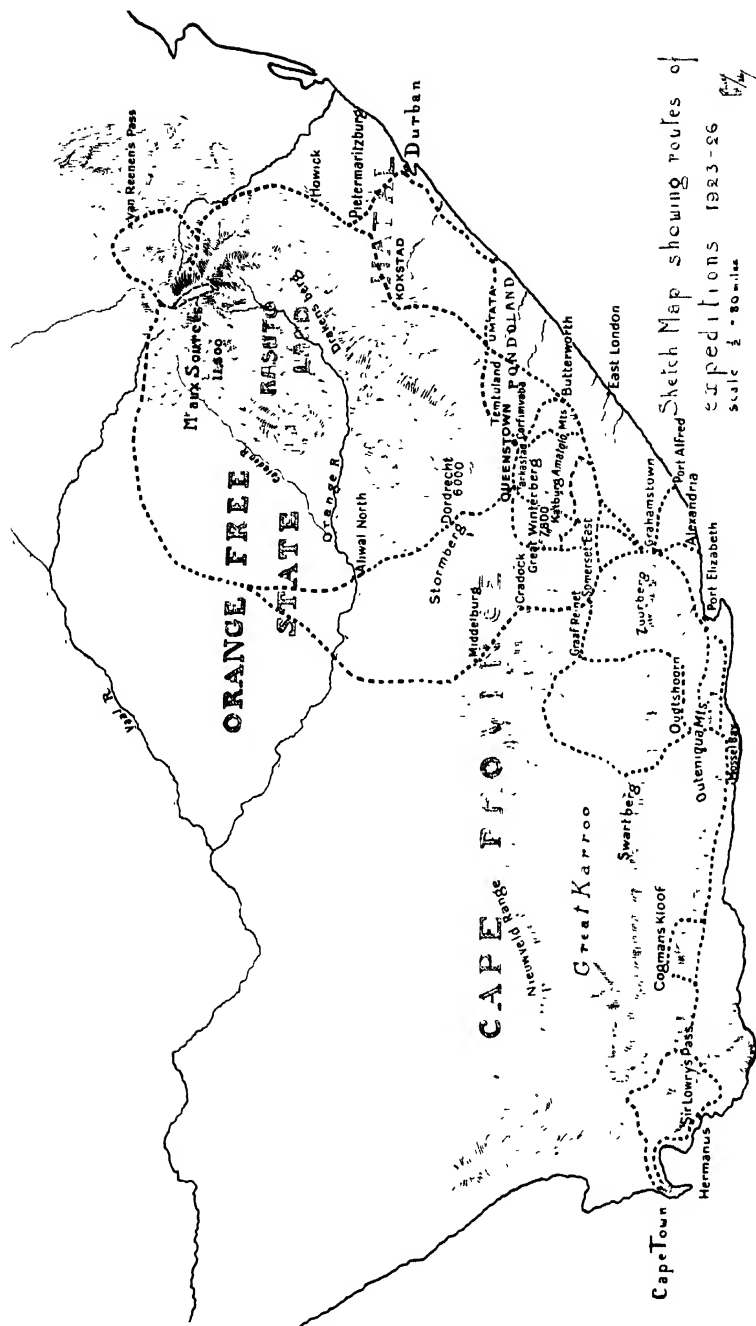
1. *CHAMÆSAURA ANGUINA*



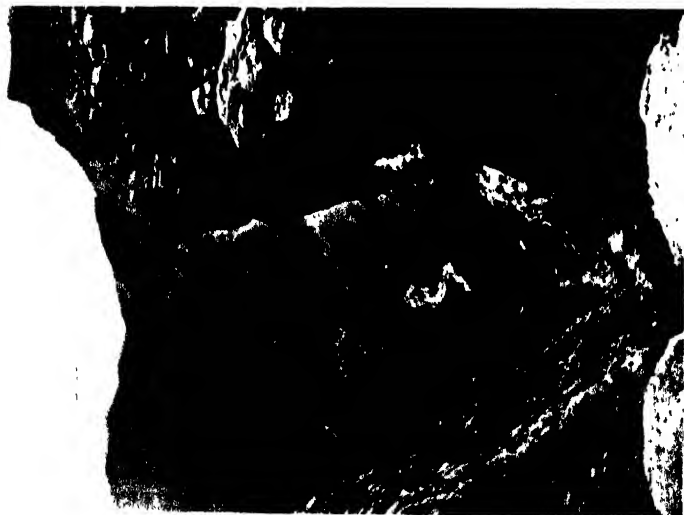
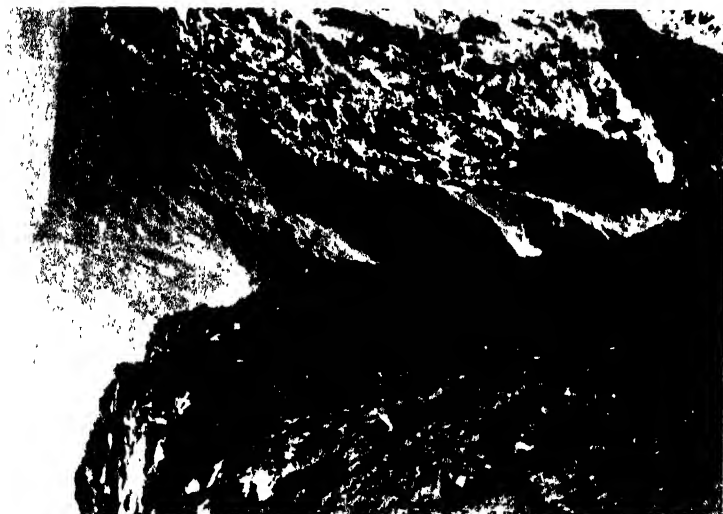
2. *PHYLLODACTYLUS FISSIPI*



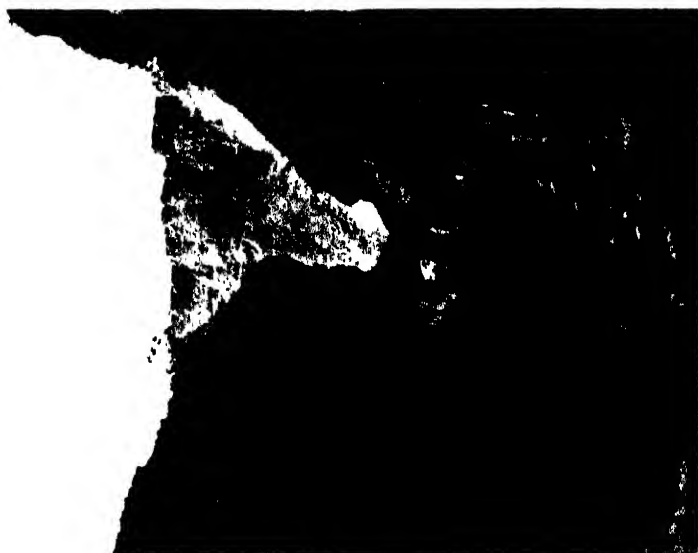
3. *ÆDURA AMATOLICA*



STUDIES IN REPTILIAN DEGENERATION



STUDIES IN REPTILIAN DEGENERATION.



STUDIES IN REPTILIAN DEGENERATION



MONT AUX SOURCES.



THE PLATEAU—11,000 FT.—RIVER TUGELA IN THE MIDDLE DISTANCE.



THE EXPEDITION AT THE SUMMIT.

From photos by Miss O. Siggs.



HOUNSLOW.—THE REPTILE SANCTUARY.

STUDIES IN REPTILIAN DEGENERATION.

45. Studies in Reptilian Degeneration.

By R. ESSEX, B.Sc.(Birm.)*.

[Received June 9, 1927: Read October 18, 1927.]

(Plates I.-VII.; Text-figures 1-86.)

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INTRODUCTION.

The present paper is a contribution to the studies of degeneration in reptiles already made by Furbringer (1869), Cope (1892), Max Müller (1900), and Camp (1923).

This work was commenced five years ago at the suggestion of Mr. J. Hewitt, Director of the Albany Museum, without whose invaluable help these studies could not have been brought to their present state. The initial stages of the work were carried out in the laboratory of Professor Duerden, of Rhodes University College, Grahamstown, during the years 1921, 1922, and 1923, and to him I am indebted for much help.

Some of the material used was generously given by the Trustees of the Albany Museum, and I have also to thank for gifts of material the Trustees of the Museums at Pretoria, Port Elizabeth, New York, Bloemfontein, Colombo, Pietermaritzburg,

* Communicated by the SECRETARY.

Kuala Lumpur, and Sheffield, and to the Trustees of the British Museum I am specially indebted for the gift of a valuable collection of *Typhlops*. To Dr. Thomas Barbour, of Harvard, I am greatly indebted for the loan of the extremely rare *Anomalepis mexicana*. Further, I owe thanks to many collectors in all parts of the world.

Most of the South African material was collected by the author, and various expeditions aggregating twenty thousand miles have been undertaken in the course of collecting material and distribution data. I have to thank the South African Government Research Board for a grant to defray the expenses of the expedition to Basutoland, and I owe a great debt to Miss O. Siggs for kindly acting as honorary photographer to the various expeditions.

All the drawings and dissections were made by the author.

Degeneration in its Wider Aspect.

Camp, in his classification of Lizards, 1923, uses the term Autarchoglossa to include all the lizards with the exception of the fossil family Ardeosauridæ, the families Gekkonidæ, Uroplatidæ, Iguanidæ, Agamidæ, and Chamæleontidæ.

This division of Autarchoglossa he subdivides into two sections: (i.) Scincomorpha, (ii.) Anguimorpha. All the members of the Autarchoglossa have such a key system of muscles as would enable them to survive should they lose their limbs.

The other division, which he calls the Ascalabotæ, have not this key system, and hence to them serpentiform degeneration is impossible.

Camp's conclusions are very sound, and his paper has been of immense value; but it contains a few slight errors, which must be mentioned, since they bear directly on the subject-matter of this paper, although they in no way detract from the excellence of his work. On page 367 he speaks of the "limbless *Evesia*" (*Acontias monodactylus*). *Evesia* has four limbs, and figure 21 b in this paper shows the pelvic girdle and hind limbs of that species.

On page 387 he gives the number of digits in *Chamæsauro macrolepis* as 1 or 2. Figures 18 and 19 of this paper show the hind limbs of *Chamæsauro macrolepis* with one or no digit, but *Chamæsauro anguina* in figures 15, 16, and 17 has one or two digits. Probably Camp means *anguina* and not *macrolepis*.

In discussing the squamation of Lizards, Camp holds that Stehli was incorrect when he held that the primitive lizards had a single row of scales to each segment, and he says that if this be true it would involve the derivation of the normal Zonurids from the degenerate *Chamæsauro*. But *Chamæsauro* is degenerate in so far as it has become serpentiform, and for the rest it should be looked on as a primitive form which at an early stage saved

itself from extinction by becoming serpentiform, but kept its primitive scaling.

The phylogeny of the Lizards does not come within the scope of this paper. The problems of degeneration have been studied along two lines: (i.) the study of the anatomy of the degenerate organs, (ii.) an intensive study of the geographical distribution of South African forms.

The Method of Degenerative Evolution.

In a paper read before the South African Association for the Advancement of Science, in 1903, on "Methods of Evolution," Prof. J. E. Duerden, in discussing the vestigial limbs and limb-girdles of various reptiles, states:—

"One becomes impressed with the small justification there is for the assumption that their retrogression is in any way associated with disuse, or that useless vestigial structures are necessarily on the road to final elimination. One seems forced to the conclusion that the degenerative changes in any particular type are the result of definite germinal changes, complete in themselves, and detached from any which have gone before or which will come after."

It is clear from the above that Duerden believes that the serpentiform lizards took to burrowing or grass-frequenting habits because they lost their limbs and not that they slowly lost their limbs because they were driven by the stress of competition to become serpentiform. Duerden lays great stress on the fixity of the degenerative stages, but if a general survey of all the degenerating or vestigial reptilian limbs or girdles be taken this impression of fixity becomes distinctly less. Certain characters may be of definite specific value—for example, the shape of the girdles in *Typhlops* (text-figs. 50-84); but when one considers that within the genus one has such a graded series showing almost every variation between *T. delalandii* and *T. mossambicus* the impression one gets is that the girdle is at present on the road to complete disappearance.

The genus *Scelotes* (text-figs. 32 & 33, and Pl. I.) provides probably the best series giving the impression of vanishing.

Scelotes capensis has five digits.

Scelotes tridactylus (*caffer*) (Pl. I. fig. 1) has three.

Scelotes bipes (Pl. I. fig. 2) has no fore limbs and a two-clawed hind limb.

Scelotes brevipes (Pl. I. fig. 3) has no fore limbs and very short hind limbs.

Scelotes guentheri has only a bud-like rudiment in place of the hind limb.

Scelotes anguina (Pl. I. fig. 4) has no external trace, but internally there is a small remnant of the femur.

Although it is perhaps impossible to find within any genus a perfectly graded series of degenerating forms, the genus *Typhlops*

provides evidence which supports the theory that such series graded by imperceptible differences have existed, and could be demonstrated if one possessed an ancestral series rather than a series of related species.

Moreover, when one considers all the figures in this work and takes into account the fact that they represent but a fraction of the total number of degraded forms, one is struck by the fact that there is represented in some species or other almost every stage from the fully developed pentadactyl limb of the *Chamaesaura cæna* to the cartilaginous scapulo-coracoid of *Acontias meleagris*.

If one holds the mutation theory to be correct, one would expect to find little or no correlation between the facts of geographical distribution and the forms of degeneration. These facts are discussed elsewhere, and although it cannot be said that all the facts of geographical distribution can be explained, yet it is obvious that an intelligent explanation of these facts can be put forward in terms of Orthogenetic Evolution, whereas the mutation theory practically ignores these facts and, if any variation is present, looks upon it as incidental.

The question arises as to how the disappearance of the girdle helps in making the "degraded" forms better adapted to their environment. A study of the musculature shows that the pectoral girdle serves as a basis of attachment for the Pectoralis, Sternothyreoideus, Supracoracoideus, Scapulodeltoideus, Brachialis, and Clavodeltoideus muscles. The muscle which is used mostly in burrowing is the Cervicomandibularis, which is attached to the inner margin of the mandible. In burrowing forms this muscle is greatly developed, while the Obliquus abdominis externus superficialis is attached to the skin and the Rectus superficialis possesses a series of slips attached to the skin to aid the animal in backward locomotion, while the Obliquus abdominis externus profundus is attached to the hinder portion of the skull. These four muscles are mainly relied on for purposes of progression by burrowing forms, and it is notable that the snake *Typhlops*, whose burrowing habits are similar to those of *Acontias* or *Amphisbana*, also resembles them in the possession of a large Cervicomandibularis muscle.

To a purely burrowing form, limbs are not only useless but tend to become a hindrance to progress, and hence one can understand their disappearance. The girdle forms the basis of attachment of the muscles used in moving the limbs, hence with the loss of the muscles the need for the girdle ceases, and, moreover, its presence would militate against the free use of the Cervicomandibularis and its associated muscles in the burrowing forms or of the anterior portion of the Rectus superficialis in the grass-frequenting forms.

Hence it follows that the absence of the girdle itself is an advantage to a form which is either burrowing or creeping.

Camp (1923) states that, from a study of his own work and that of Fürbringer, Müller, Rabanus, Goette, and Bogoljubsky, he was struck by the similarity between the extreme degenerative series and the early embryonic stages in such elements as the sternum and scapulo-coracoid, and he mentions the following facts:—

1. Fürbringer's drawing of the sternal remnants in *Blanus trauchii* agrees with Bogoljubsky's figure of the embryonic condition.

2. The interclavicle appears last in the embryology and disappears first.

The clavicle is the next in turn each way in Scinomorphs. The sternum disappears before the scapulo-coracoids and appears later in the embryo; before final reduction it takes on the form of a parasternal chevron, and at the final end stages may resemble such fragments as are seen in the embryology of the salamanders.

The similarity between the degenerative and embryonic series is, to my mind, so striking as to preclude all other explanations but that they are one and the same, and the so-called degenerating girdle is merely an arrested embryonic stage, and the arresting gets progressively earlier as the changing habits prove advantageous.

Duerden thinks that degenerative changes are due to germinal changes. It is more probable that the germinal changes are the result of degeneration.

The Limbs and Limb-girdles in the Genus Chamæsauro.

The genus *Chamæsauro* is to be regarded, from a study of its scaling, as the most primitive of the Zonuridae. Three species (*C. ænea*, *C. anguina*, and *C. macrolepis*) are found in South Africa, and the geographical distribution of these species points to the conclusion that most of the degeneration evident in the genus has occurred in Africa, probably south of the Zambesi.

CHAMÆSAURA ÆNEA.

In this species the limbs have undergone distinct reduction in size, but remain pentadactyl. The tail, as is common in most grass-frequenting serpentiform lizards, has become greatly elongated, and may comprise almost three-quarters of the total length. It has been sometimes assumed that the minute limbs of various serpentiform lizards are functionless, but an examination of various types in the field has shown that species with very degenerate limbs still use them. Two adult specimens measured had a total length of 460 mm. respectively, and the fore limbs in each case measured 11 mm. and the hind limbs 14 and 16 mm. respectively.

This species is found in the Drakensberg area.

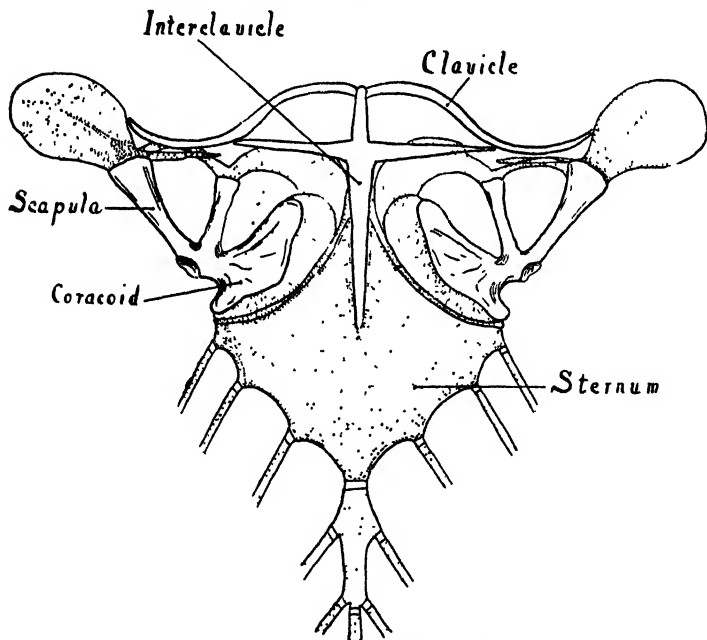
CHAMÆSAURA ANGUINA.

The limbs here are more reduced than in *œnea*, and average 6 mm. in the fore limb and 8 mm. in the hind limb. They are smaller in proportion to the body and are styliform, but with a slight bend at the elbow- and knee-joints. Usually the limb terminates in a single minute claw. This species inhabits the region of South Africa south of the Drakensberg.

CHAMÆSAURA MACROLEPIS.

This is the most specialized species, and is found only in Zululand and Natal. The fore limbs are absent altogether, and the hind limbs are styliform and sometimes terminate in an extremely minute claw.

Text-figure 1.

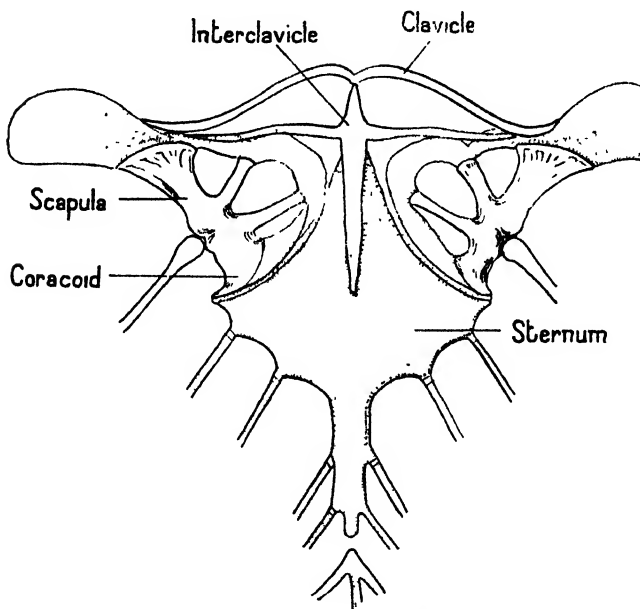
Pectoral girdle of *Chamæsaura œnea*.*The Pectoral Girdles.*

Text-figs. 1-3 represent the pectoral girdles of the three species. In each case the sternum is well developed and there is present a distinct xiphisternum and parasternum or series of abdominal ribs. These abdominal ribs occur among the

Anguimorpha only in the subfamily *Chamaesaurinae*, although they have been recorded in all known Scincidae, Anelytropsidae, Feylinidae, and Dibamidae.

Camp, in his classification of Lizards (Bull. A. M. N. H. vol. xlviii. 1923), speaks of the "... progressive increase in the number of parasternal ribs in series of autarchoglossine forms having a progressively burrowing habitus." Neither girdle possesses a sternal fontanelle. In the girdle of *C. aenea* there are two scapulo-coracoid fenestrae, in *C. anguina* there are three. In *C. macrolepis* the scapulo-coracoid shows distinct signs of

Text-figure 2.



Pectoral girdle of *Chamaesaura anguina*.

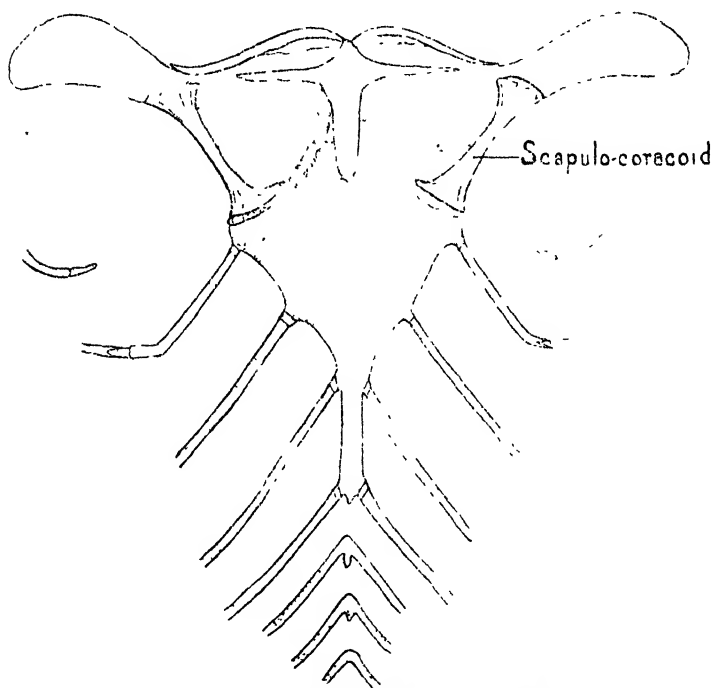
degeneration in so far that no trace of a glenoid cavity is present and the scapular and coracoidal processes which enclose the scapulo-coracoid fenestrae are cartilaginous. In this species the cruciform interclavicle is proportionally smaller.

The pelvic girdles show a good deal of variation. Text-fig. 4 *a* shows a normal girdle of *C. aenea*. Text-fig. 4 *b* shows a girdle with a very wide epipubic cartilage. In both the hypischium is well developed. Text-fig. 5 *b* shows a normal girdle of *C. anguina*. Fig. 5 *a* is interesting owing to the unusual shape of the epipubic cartilage.

Only in the Varanidae among the lizards is the epipubic bone

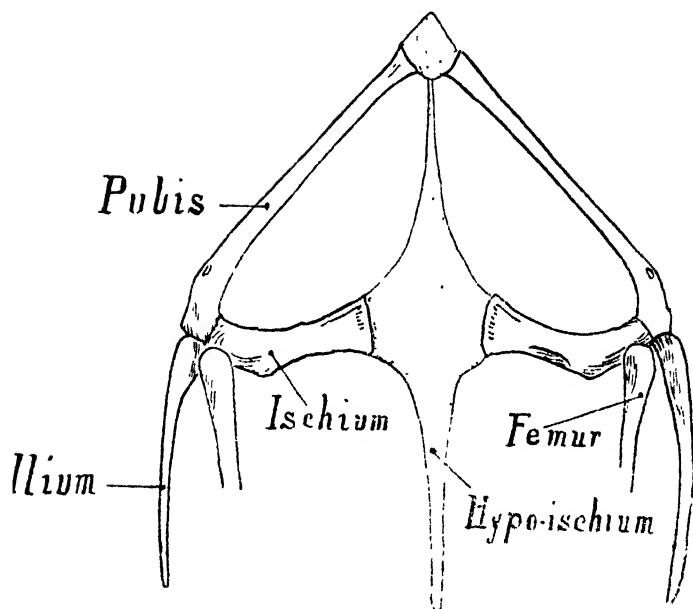
paired, and the girdle here figured is the only one I have seen with this exceptional pseudo-pairing of the cartilage. The pelvic girdle of *C. macrolepis* differs very much from that of *C. ceneo* and *C. anguina*. The *pubes* and *ischia* are almost parallel, and, as Cope noticed (Cope, 1894, pl. xiii. fig. 1 b), the hypoischium is very elongated. The hypoischium was once thought to represent the phylogenetically oldest portion of the girdle; but Mehnert doubted this, and asserted that the hypoischium was not a separate structure, but that it and the ligamentum hypoischium

Text-figure 3

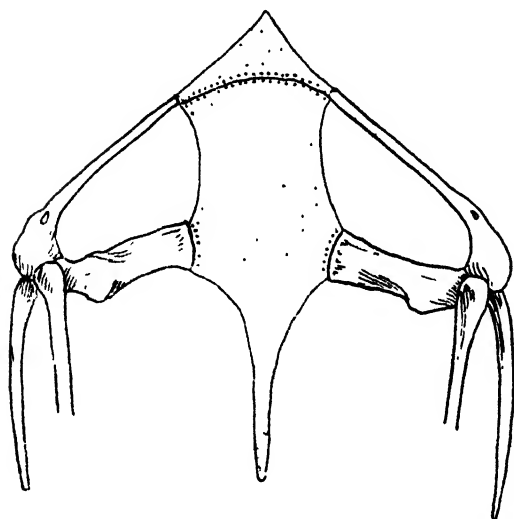
Pectoral girdle of *Chamasauro macrolepis*.

were merely prolongations of the original ischial cartilage. If this be so, its late origin would probably cause its early disappearance when degeneration sets in. But apparently it shows less tendency to disappear than do other parts of the girdle. Camp (Class. of Lizards, Bull. A. M. N. H. vol. xlviii. 1923) suggests that the structure is not a primitive degenerating element, but only an epiphysial calcareous deposition in the ligamentum hypoischium. If this be proved, its persistence might possibly be explained. A microscopical examination of the fore limbs

Text-figure 4 a.



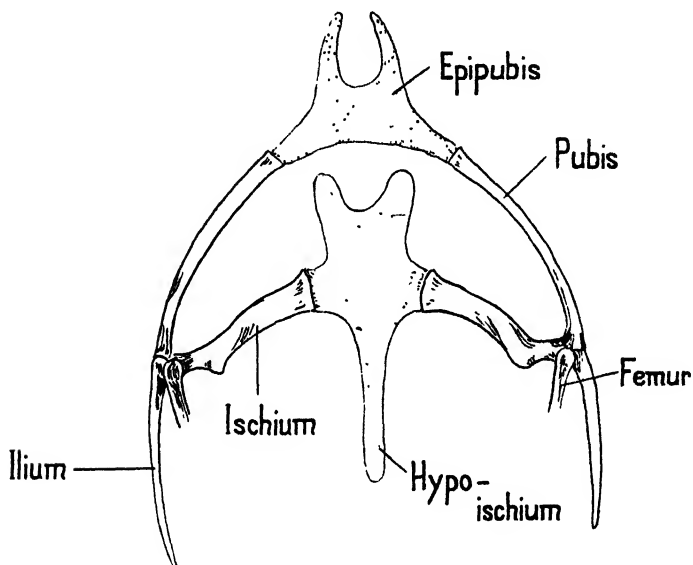
Text-figure 4 b.



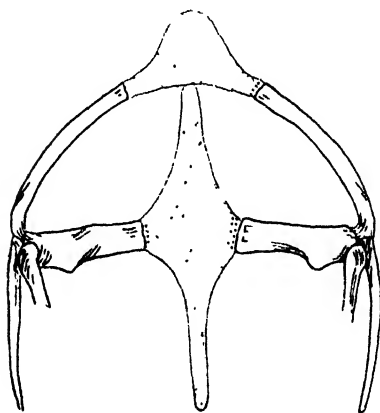
Figs. 4 a & 4 b.—Pelvic girdles of *Chamaesaura aenea*.

revealed a good deal of variation in the carpal bones. Text-fig. 7 shows an almost typical lacertilian carpus with an ulnare, tibiale,

Text-figure 5 a.



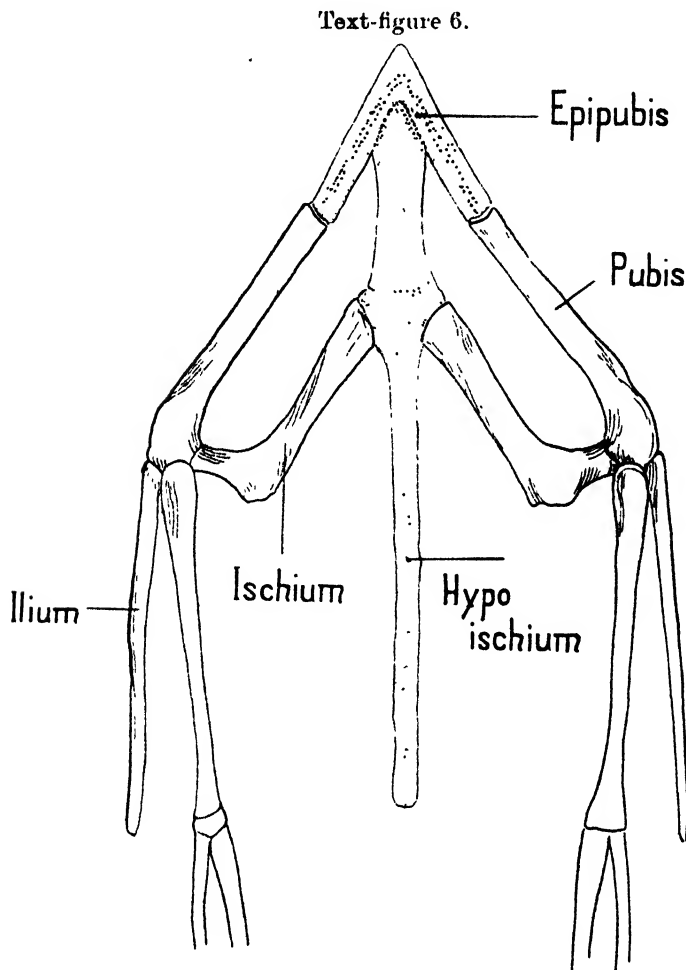
Text-figure 5 b.



Figs. 5 a & 5 b.—Pelvic girdles of *Chamasauro anguina*.

centrale, intermedium, four proximal carpals, and a phalangeal formula 2, 3, 4, 5, 3. In text-fig. 8 the metacarpal of the fifth

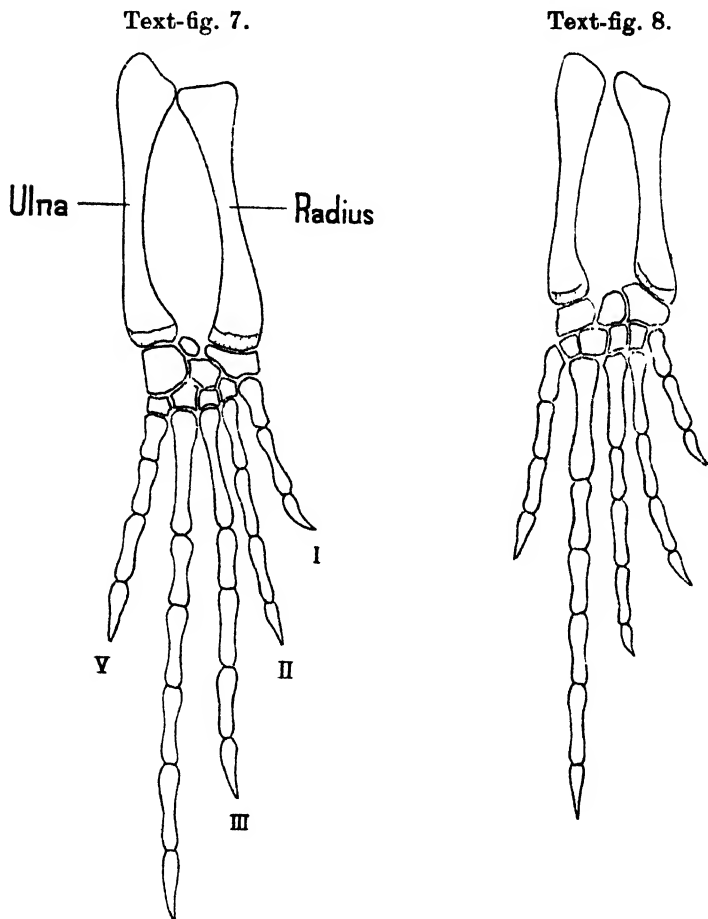
digit articulates with the outer edge of the fifth carpal, and there is no intermedium. Text fig. 10 also has no intermedium, and the radiale is very reduced, while in text-fig. 9 the third, fourth, and fifth carpals are fused. Without attempting to place these



Pelvic girdle of *Chamasauro macrolepis*.

in any orderly series of degeneration, it yet appears significant that a great amount of variation should be shown in a species whose nearest allies show marked degeneration. A study of the four hind limbs, shown in text-figs. 11-14, shows a similar state of affairs.

Text-figs. 15, 16, & 17 show that the limbs of *C. anguina* give evidence of much more variation. In the hind limb it has been possible to arrange a graded series showing the trend of degeneration. It might be argued that this series is factitious, and such an argument might be tenable if the specimens dissected



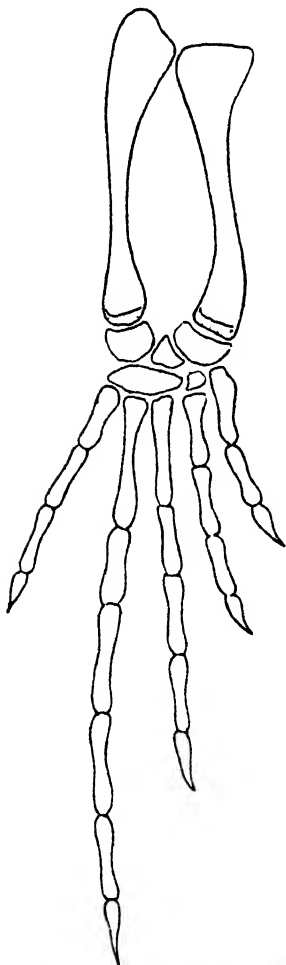
Figs. 7 & 8.—Fore limbs of *Chamæsauro aenea*.

had come from a single small area; but, since the range of geographical distribution covers a distance of about 800 miles, it is permissible to hold that these do not represent the result of the intermingling of two extremes, but do actually represent an evolutionary series and tend to show that the 3rd digit is at

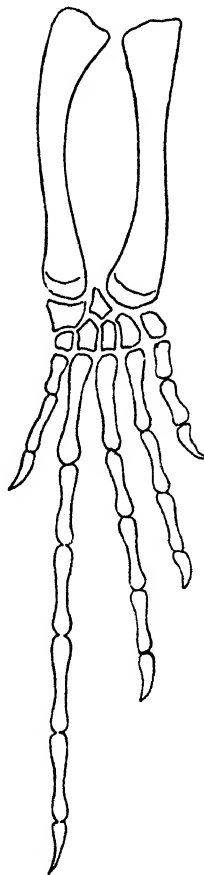
the present time in the process of being eliminated by almost imperceptible degrees.

Text-fig. 17 represents four limbs of very young *C. anguina*

Text-fig. 9.



Text-fig. 10.

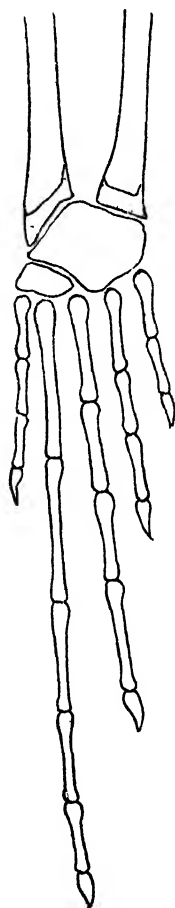


Figs. 9 & 10.—Fore limbs of *Chamaesaura anea*.

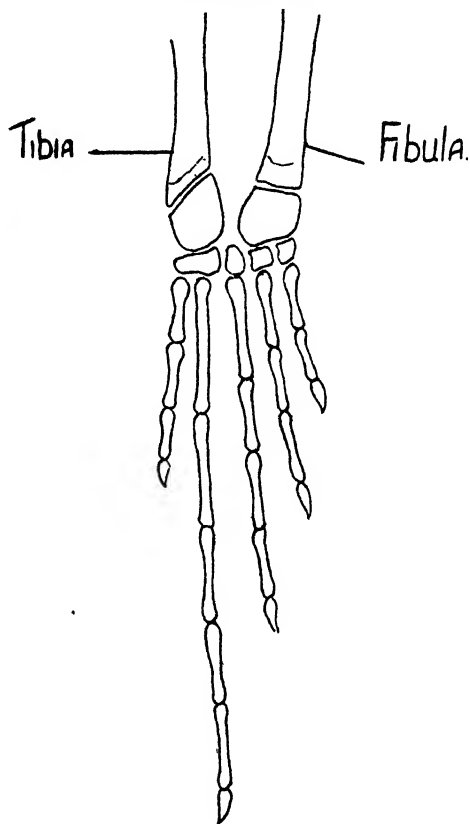
specimens, and in each of the fore limbs there appears a remnant of the 4th carpal. It would be interesting to discover whether embryological evidence is constant on this point.

Two specimens of *C. macrolepis* (text-figs. 18 & 19) from Zululand were dissected, and it is noteworthy that one has a single digit possessing three phalanges, while the other has no remnant of a digit, there being merely a cartilaginous knob which may be the 3rd metatarsus. Here, again, the variation is

Text-fig. 11.



Text-fig. 12.

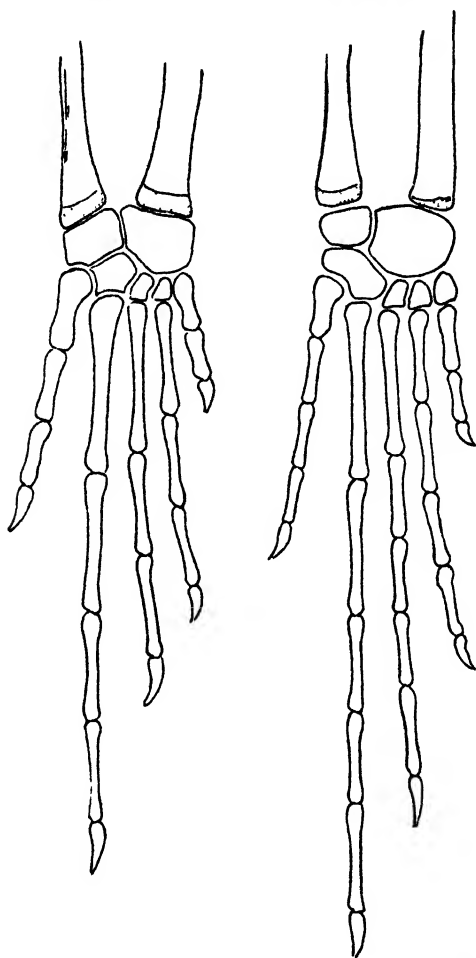
Figs. 11 & 12.—Hind limbs of *Chamasaura anea*.

significant, and it would appear that *C. macrolepis* is still in a stage of degenerative evolution, but, unfortunately, in this case the geographical distribution data is of no help, since *C. macrolepis* is only known from the rather small area of Zululand and Natal.

A consideration, therefore, of the anatomy of the degenerate limbs of the genus *Chamaesauri*, taken together with the facts of the geographical distribution, which will be discussed later

Text-fig. 13.

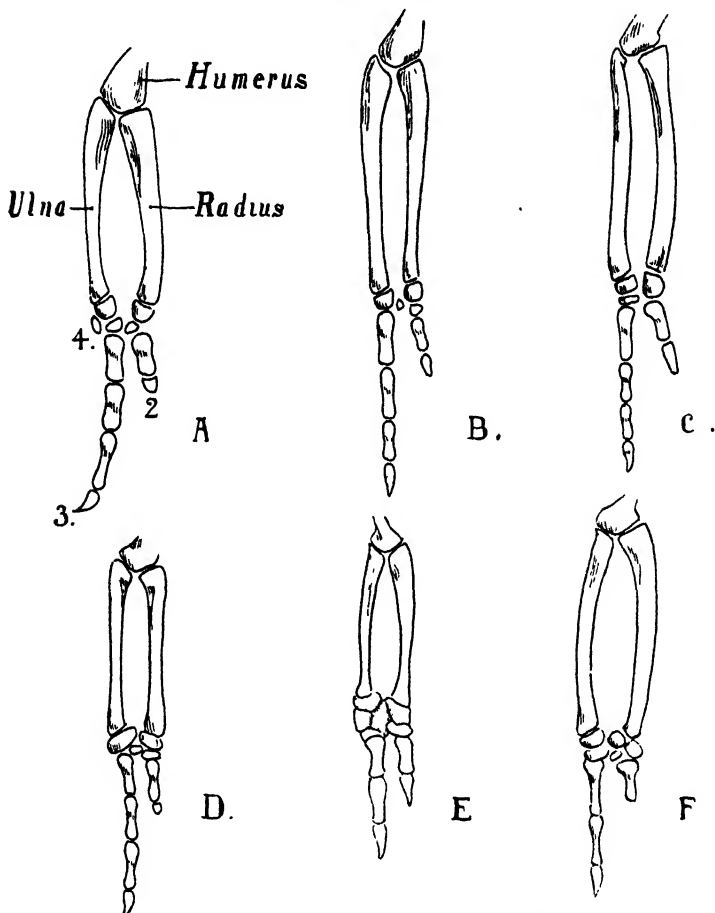
Text-fig. 14.

Figs. 13 & 14.—Hind limbs of *Chamaesaura ansea*.

forces one to the conclusion that the species, although representing different evolutionary stages whose origins may be separated in time, probably by very long periods, are yet all tending in the same degenerative direction, and hence the probability is

that *anguina* had previously an *cæna* stage and *macrolepis* had probably an *anguina* and an *cæna* stage, just as each had once more normal Zonurid proportions.

Text-figure 15.



A-F. Fore limbs of *Chamaesaura anguina*.
Showing variation in the degree of degeneration.

The Limb-girdles in the Genus Acontias. (Text-figs. 20-28.)

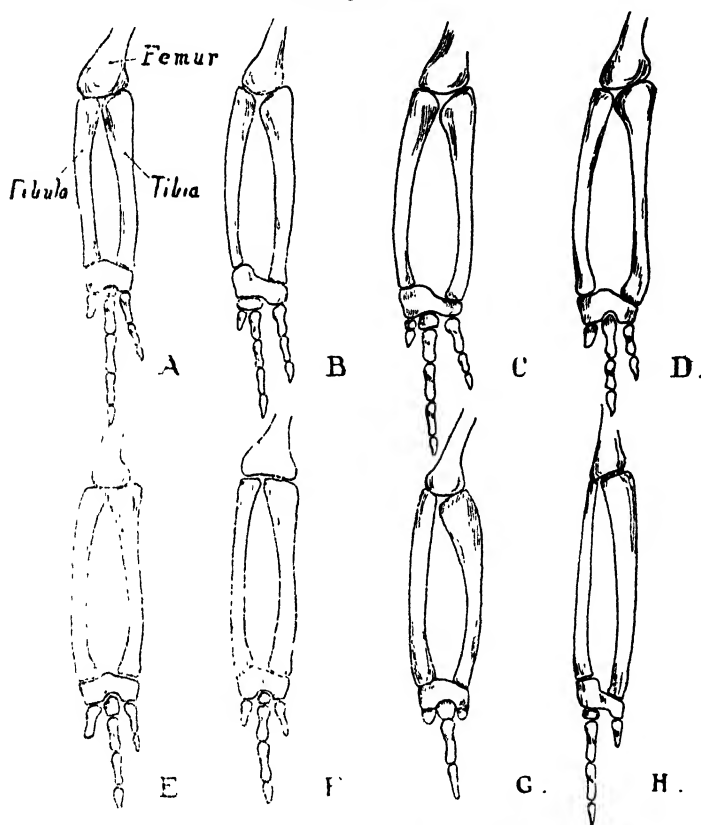
In a paper * written in conjunction with Prof. J. E. Duerden in 1923 the author made the following remark: "Working with us," Mr. V. FitzSimons has found a corresponding fixity in the

* S.A. Journ. Nat. Hist. vol. iv. no. 3, p. 183.

stage of degeneration of the limb girdles in the South African slow-worm, *Acontias meleagris*." Further work of a much more extensive nature makes it necessary to qualify this statement.

In 1925 the author described two new species, *A. breviceps* and *A. gracilicauda*, and an examination of the specimens in the

Text-figure 16.

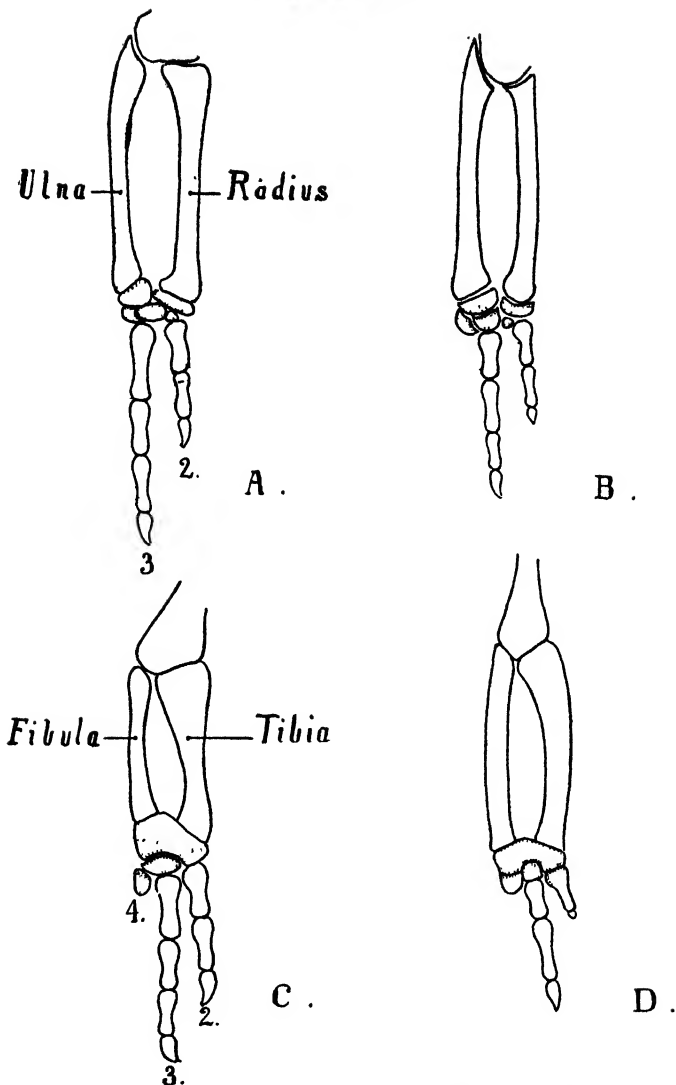


A-H. Hind limbs of *Chamaesaura anguina*.
Showing variation in the degree of degeneration.

Albany Museum, in the South African Museum, and in the author's own collection led to the conclusion that the genus was in need of revision. This revision is at present in hand.

An examination of the South African Museum specimens identified by Boulenger showed two types: (1) a fat-tailed variety

Text-figure 17.



A & B. Fore limbs of very young specimens of *Chamaesaura anguina*.

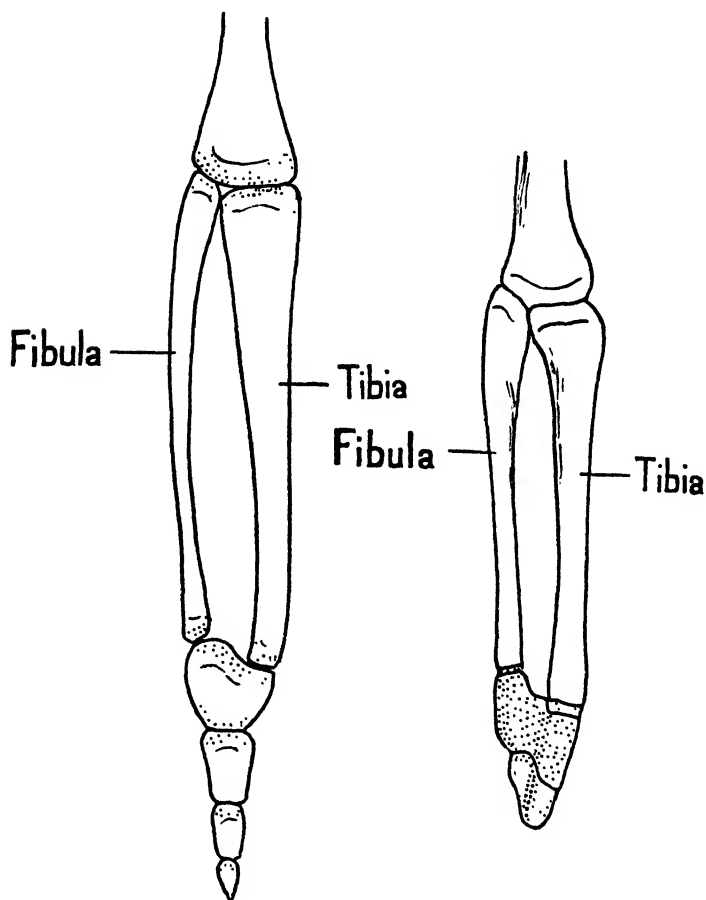
C & D. Hind limbs of very young specimens of *Chamaesaura anguina*.

with an interparietal head-shield in the shape of an equilateral triangle, and (2) a thin-tailed one with a narrower interparietal. The fat-tailed ones came from districts west of a line drawn

from Graaf Reinet to Port Elizabeth, excluding Namaqualand, and the thin-tailed ones came from districts east of the same line and from Namaqualand. Hence it was apparent that one was dealing with two species or at least varieties. For the purpose

Text-fig. 18.

Text-fig. 19.



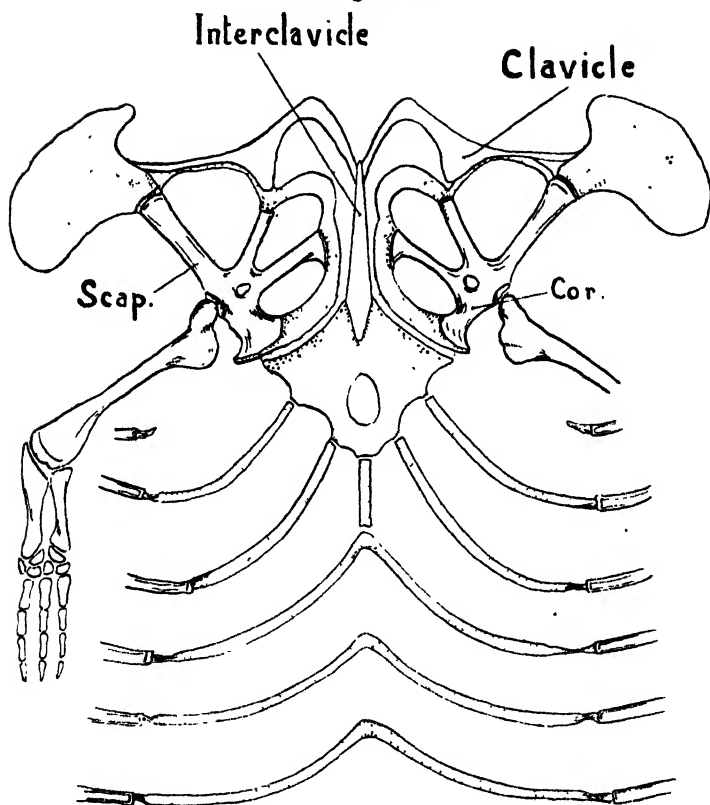
Figs. 18 & 19.—Hind limbs from two specimens of *Chamaesaura macrolepis*.
The corresponding limb from each specimen showed no variation.

of this paper the name *A. meleagris* (a) is given to the fat-tailed, of which Boulenger identified 28 specimens in the South African Museum, and the term *A. meleagris* (b) is given to the thin-tailed, of which he identified 16 specimens.

There have been dissected the following species :—

<i>Acontias meleagris</i> (a)	30
<i>Acontias meleagris</i> (b)	3
<i>Acontias breviceps</i>	2
<i>Acontias gracillicauda</i>	1
<i>Acontias monodactylus</i>	1
<i>Acontias burtonii</i>	1
<i>Acontias lineatus</i>	1

Text-figure 20.



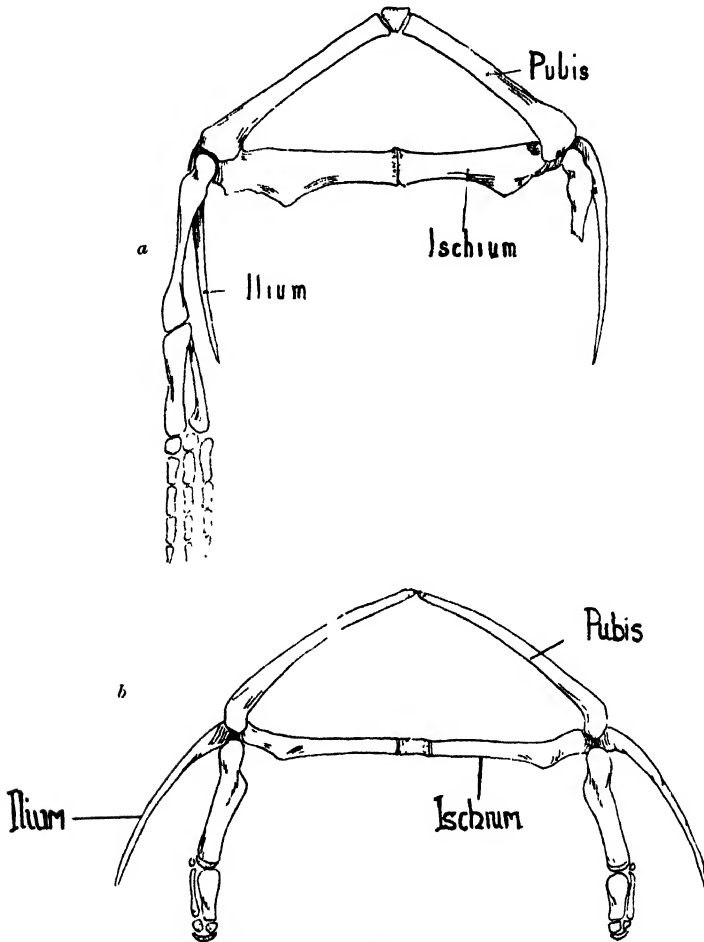
Pectoral girdle of *Acontias burtonii*.

From a specimen kindly presented by the Ceylon Museum.

Text-figures 25 *b* & 26 show dissections of *A. meleagris* (a). Text-fig. 25 *b* has cartilaginous scapulo-coracoids, and text-fig. 26 has these bones ossified. In every case there were 23 parasternal ribs, thus agreeing with Camp (Class. of Liz., Bull. A. M. N. H. vol. xlviii. pt. xi. p. 387, 1923); but in no two cases were the

remnants of the parasternum similar, consequently the remark quoted above anent the fixity of the degenerative stage of the pectoral girdle of *A. meleagris* is true only in so far as it concerns

Text-figure 21.



a. Pelvic girdle of *Acontias burtoni*.

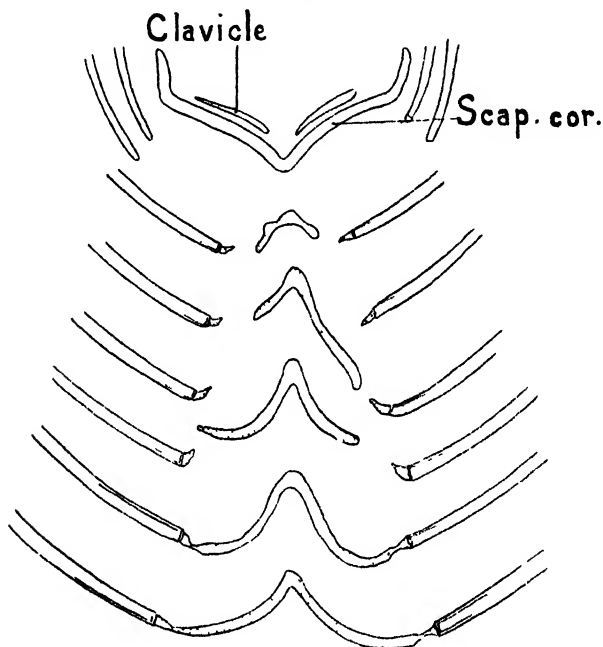
b. Pelvic girdle of *Acontias monodactylus*.

From specimens kindly presented by the Ceylon Museum.

the *shape* of the scapulo-coracoids. If the ossification or otherwise be taken into account or if the parasternum be considered, then one cannot say there is a fixity. The shape is undoubtedly fixed, and can be considered as of help in determining the species.

Text-fig. 25 *a* shows the girdle of *Acontias meleagris* (b). As in *A. meleagris* (a), the parasternum is very degenerate and asymmetric. The scapulo-coracoids are more robust than in *meleagris*, and remnants of the clavicles are present. Text-fig. 24 gives the girdle of *A. gracilicauda*, which shows fairly large clavicles. *A. breviceps* (text-fig. 22) has a girdle in which the inner ends of the scapulo-coracoids join in the median line and the outer ends make a distinct angle. The clavicles are well represented. *A. plumbeus* (text-fig. 23) has two well-ossified scapulo-coracoids and remnants of the sternum, but has no

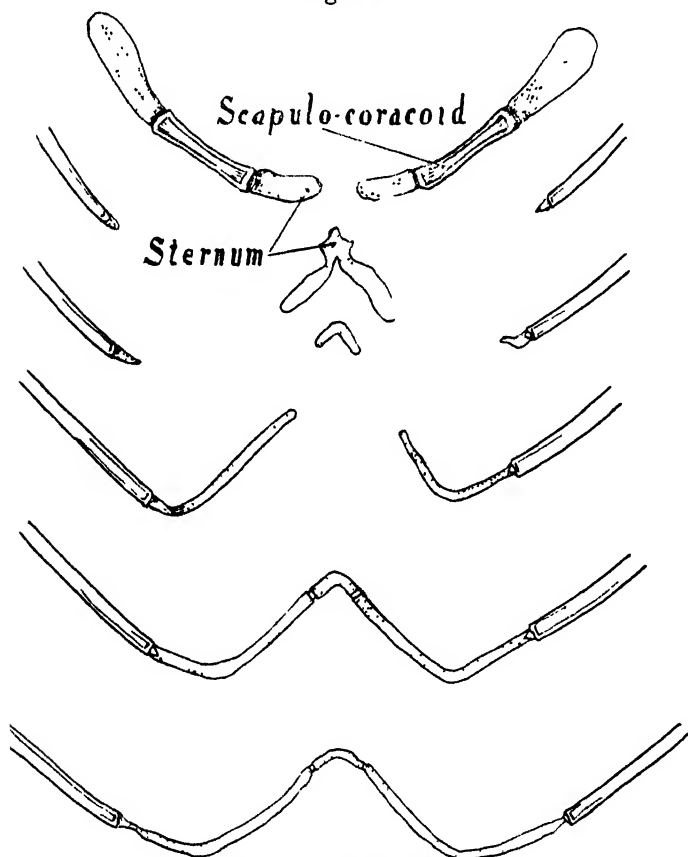
Text-figure 22.

Pectoral girdle of *Acontias breviceps*.

clavicles. *Acontias burtonii* from Ceylon is the least degenerate member of the genus. It and *A. monodactylus* are nearly related. Boulenger placed these two species in the genus *Acontias* on the ground that, in common with *A. meleagris*, *plumbeus*, *lineatus*, etc., they have a suture running from the nostril to the posterior edge of the rostral. This seems to the author hardly sufficient to warrant their inclusion in the genus when the difference in head-shields is taken into account. *A. burtonii* has an almost complete girdle, but is in several respects peculiar. The inter-clavicle is not cruciform as in typical skinks, but is reduced to a

longitudinal bar as it is in its nearest relative, *Acontias monodactylus* (Cope, 1892 b, fig. 9). In this it resembles the Teiids, as shown in *Bachia intermedia* (Camp, loc. cit. fig. 68). The clavicle is rather hook-shaped, and has a large projection meeting the first proscapular process. Camp considers the hook-shape as one of the first real steps in the degeneration of this bone,

Text-figure 23.

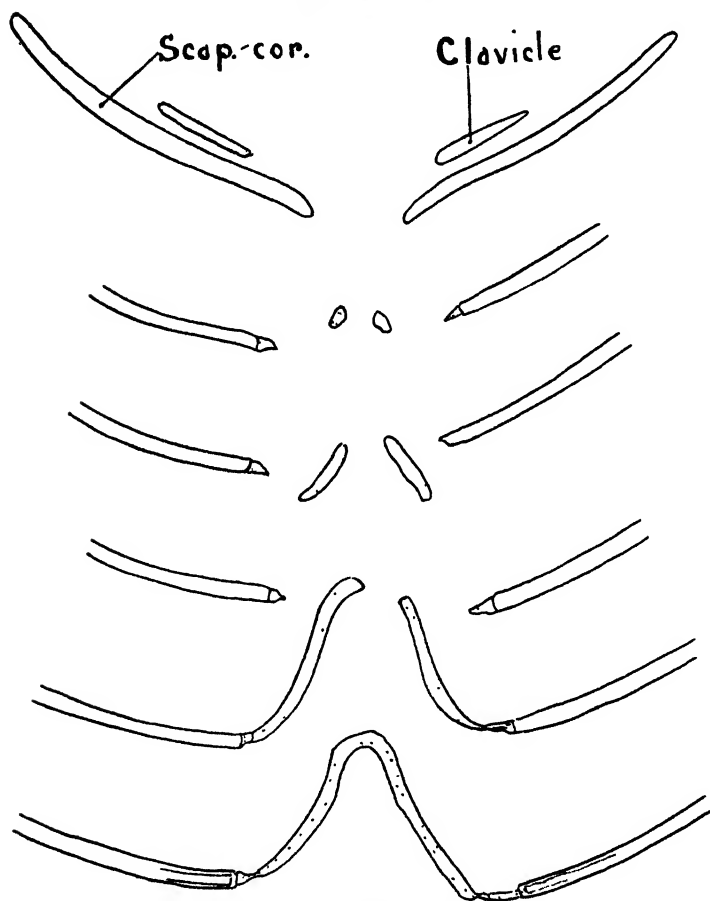
Pectoral girdle of *Acontias plumbeus*.

and is of the opinion that this is due to the development of the clavodeltoideus muscle. The first step apparently is the development of a perforation. The stage reached by *A. burtonii* is therefore the second step, since it is fairly obvious that if the posterior margin of such a perforation as that in the clavicle of *Xantusid vigilis* vanishes there remains a shape such as that found in *A. burtonii*.

Girdles and Limbs of Scelotes caffer (text-fig. 29) and *Scelotes* (*Herpetosaura*) *anguina* (text-figs. 30, 32, & 33).

Scelotes caffer is a degenerate Scincoid (Pl. I. fig. 1). The specimen dissected was taken near Fort Brown in the Albany District

Text-figure 24.

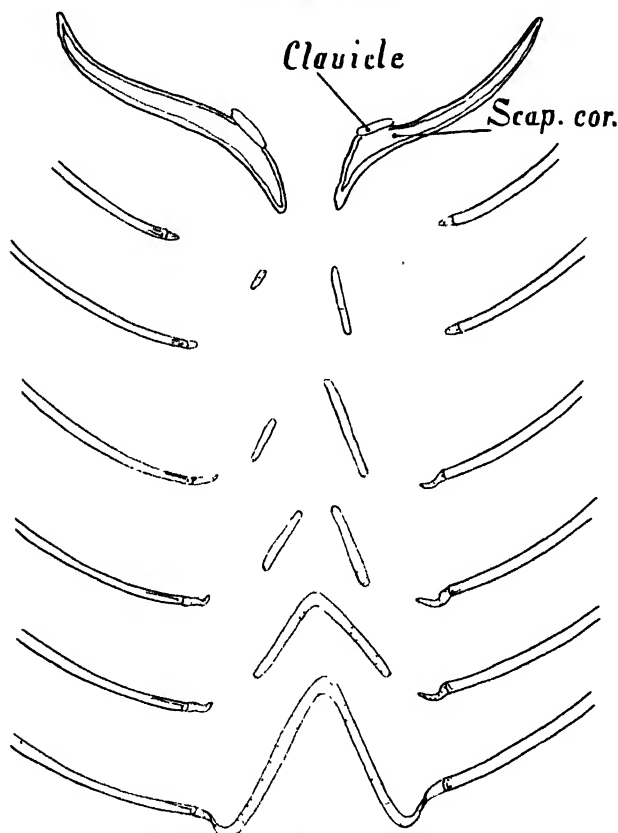


Pectoral girdle of *Acontias gracilicauda*.

of Cape Province, in what is known as Karroo Country. The four limbs are extremely small but still functional, and even when the animal progresses by means of a snake-like motion, the limbs perform the ordinary "walking" movements, and when resting the animal frequently raises its body by means of these degenerate limbs.

The pectoral girdle is interesting, since it shows little degeneration except in the sternal ribs, where, owing to a shifting from the left to the centre, the parasternum has become asymmetric. The fore limb shows three digits and the phalangeal formula is 2, 3, 3. It is probable that these digits represent the second, third, and fourth of the normal lacertilian hand. A distinct

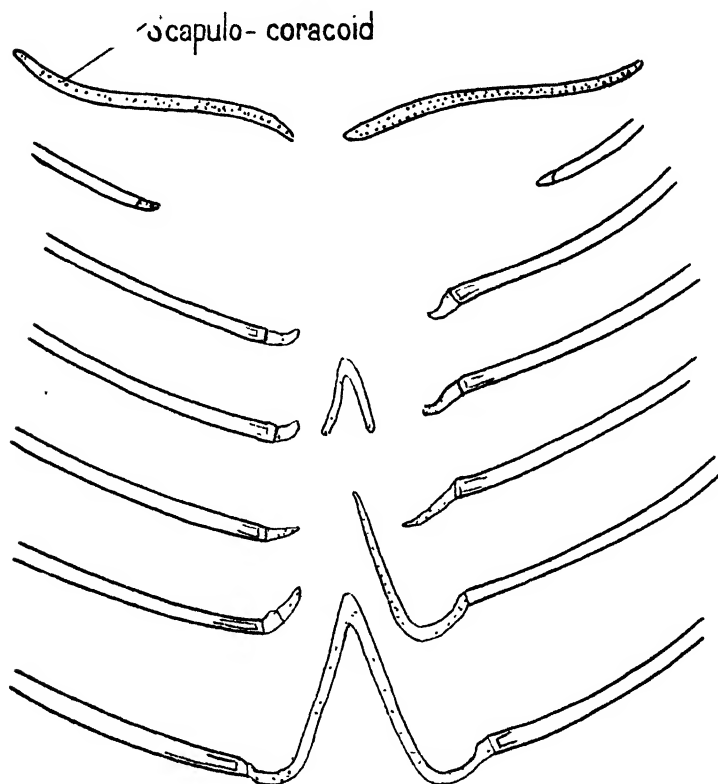
Text-figure 25 a.

Pectoral girdle of *Acontias meleagris* (b).

amount of fusion and loss has gone on in the carpus, and the large central bone is probably the fused radiale, intermedium, and carpalia 2 and 4. The ulnare still remains, and the small bone on the outer side may be the carpal of the lost fifth digit. The hind limb has three digits with a similar phalangeal formula 2, 3, 3, and the tarsus shows almost as much fusion and loss as the carpus. The pelvic girdle (text-fig. 31) is simple and

triangular, and seems to have undergone general reduction. The epipubic cartilage is a simple rhomboid structure, but the hypischium, which in *Chamcesaura macrolepis* is very long, is absent altogether, and the ischia do not meet.

Text-figure 25 b.

Pectoral girdle of *Acontias meleagris* (a).

The Girdles of Scelotes anguina. (Text-figs. 30, 32, & 33.)

Hewitt* considers that it is undesirable to maintain the genus *Herpetosaura*, but to refer species hitherto regarded as belonging to that genus to the genus *Scelotes*. I have therefore not used the name *Herpetosaura anguina* Boulenger, but have followed Hewitt in considering this species as a very near relation of *Scelotes caffer*.

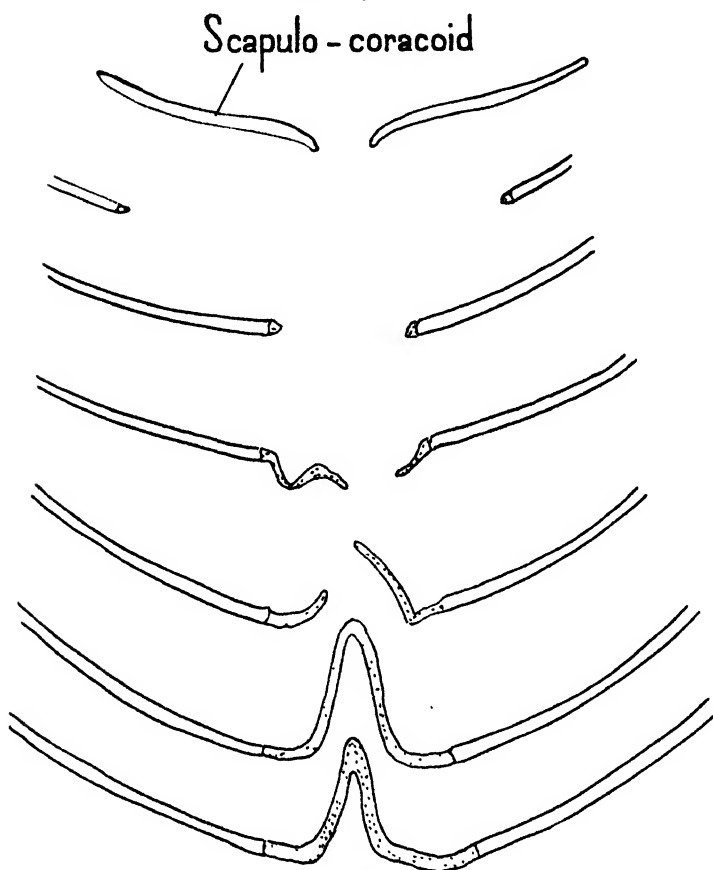
The two specimens collected came from Port Elizabeth. The

* Hewitt, 'Annals of Durban Museum,' vol. iii. part 1, 1921.

species is entirely limbless, and no external trace of either pectoral or pelvic limbs is visible.

The pectoral girdle shows marked degeneration. The clavicle is well developed and the cruciform interclavicle is even better developed than in *Scelotes caffer*, but the scapulo-coracoid is

Text-figure 26.



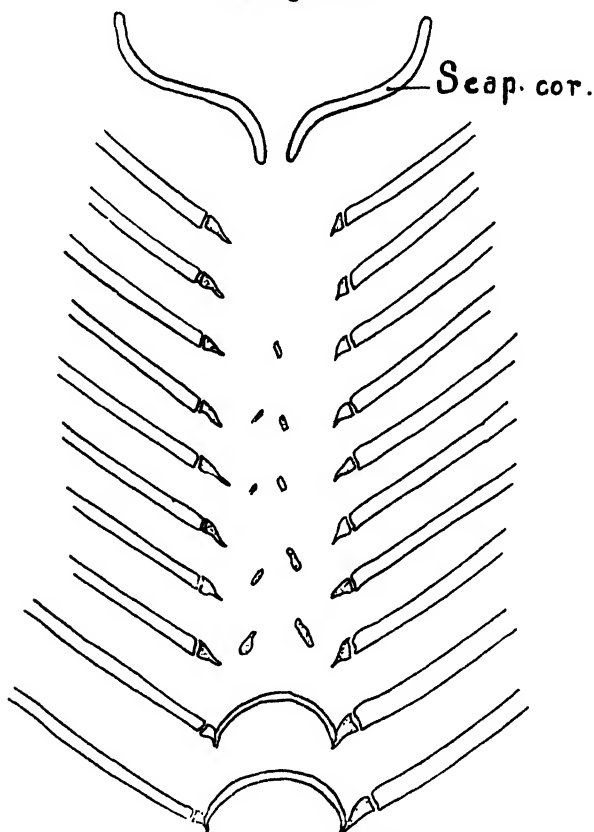
Pectoral girdle of *Acontias meleagris* (a).

a simple bar. There is no trace of a glenoid cavity or of a scapulo-coracoid fenestra, and the girdle is quite symmetrical and the sternum contains no fontanelle. The pelvic girdle is remarkable in so far that each of the two specimens dissected possessed extremely minute but undoubted remnants of the femur.

The Limb-girdles in Feylinia currorii. (Text-fig. 34.)

Rabanus (1906-1915, pl. xxiii. fig. 33) figured the girdle of this species. From his figure it can be seen that the scapulo-coracoids are present, and lying near to them are the remnants of the clavicles. The sternum is present but very small, and Camp ("Classification of Lizards," Bull. A. M. N. H. vol. xlviii.

Text-figure 27.

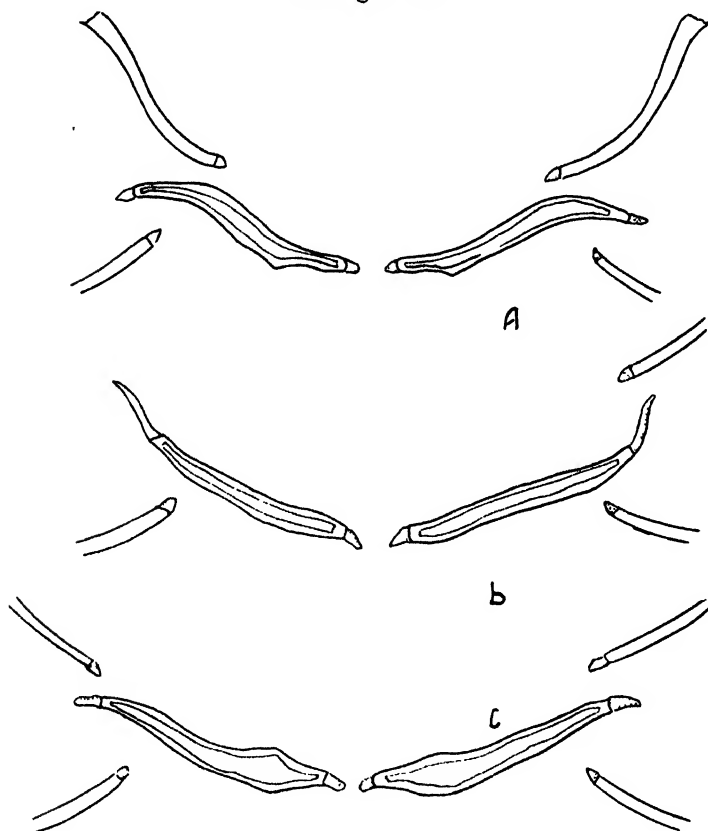
Pectoral girdle of *Acontias lineatus*.

1923) states that there are 35 pairs of parasternal ribs present together with a few irregular pieces. Müller (1900) and Rabanus also find 35 pairs. I have also found 35, and have figured my dissection of the girdle of a specimen kindly given by the American Museum of Natural History. A comparison of my drawing with that of Rabanus shows that the sternum is still further reduced, being separate from the right scapulo-coracoid

but the connection with the first right parasternal rib is stronger than in Rabanus's figure. Moreover, the clavicles represented in his figure are certainly more robust than those in my specimen.

The data here are rather meagre, but it is noteworthy that these degenerate structures again show variation and asymmetry. The

Text-figure 28.



- a. Pelvic girdle of *Acontias gracilicauda*.
- b. Pelvic girdle of *Acontias meleagris* (n).
- c. Pelvic girdle of *Acontias plumbeus*.

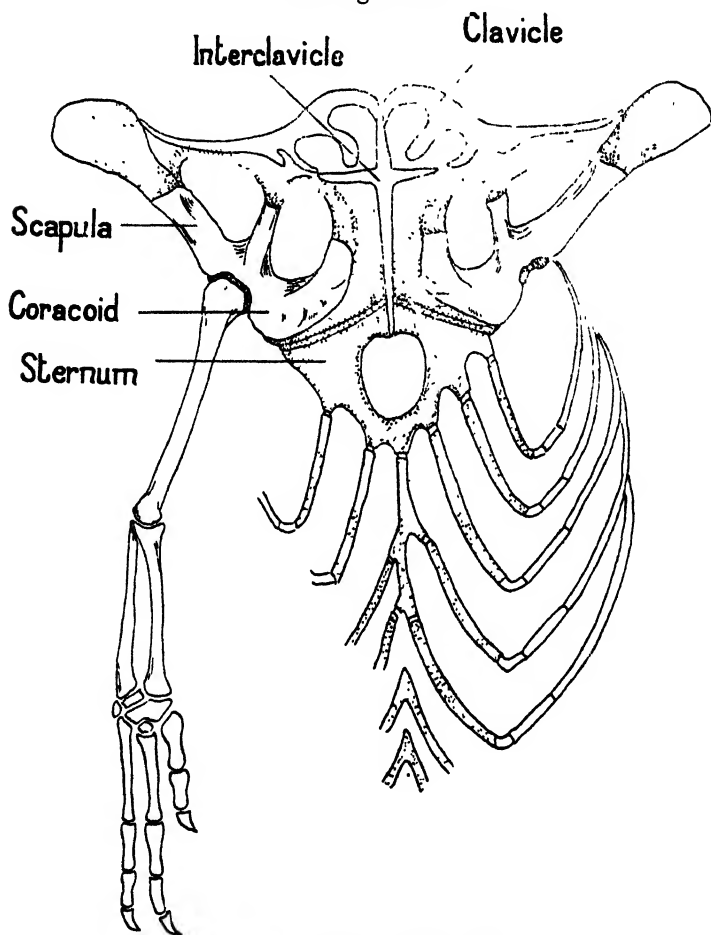
pelvic girdle consists of two bones lying just anteriorly to the cloaca in the same position as in *Acontias*, and here again one surmises them to be *ischia*.

Text-figs. 35-38 show the Pelvic girdles and the limbs of *Tetradactylus africanus*. It is thought advisable to discuss these only when the other species have been dissected.

The Pelvic Girdle of the Snake Glauconia.

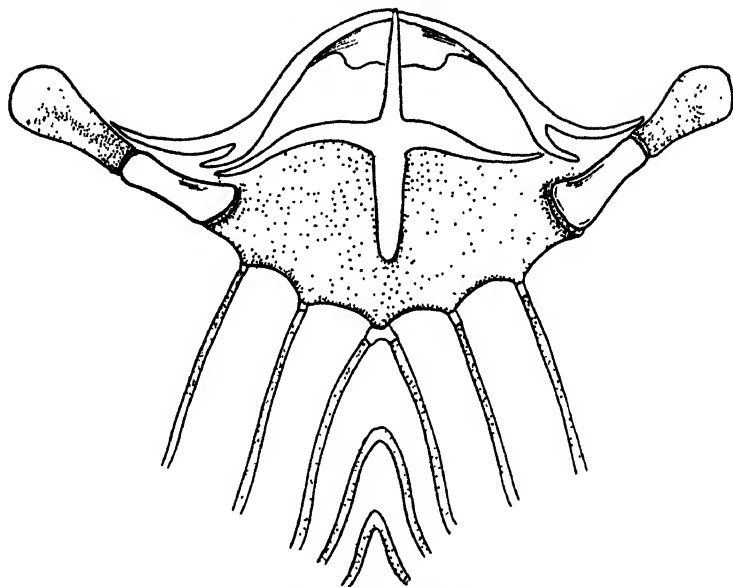
The genus *Glauconia* consists of 46 species, all of which are tropical or sub-tropical in their distribution. They are small, burrowing, worm-like animals and are insectivorous in habit.

Text-figure 29.

Pectoral girdle of *Sclotes caffer*.

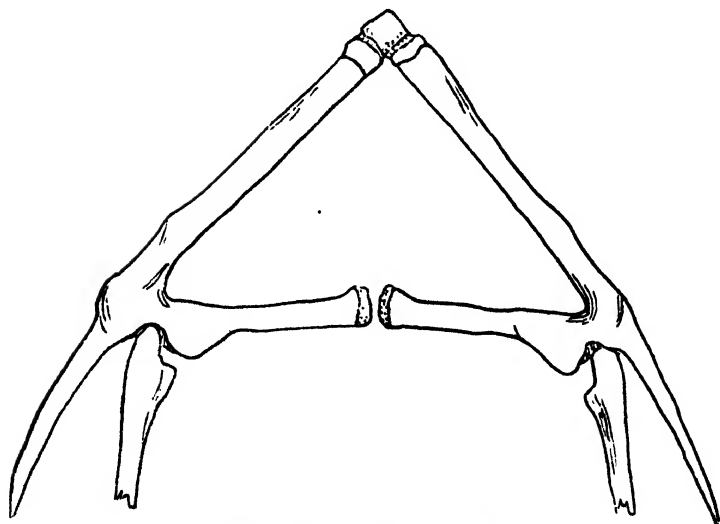
They bear a very close superficial resemblance of the Typhlopidae, but they differ in so far as the nasal shield in *Glauconia* always borders the lip and the preanal shield is always enlarged. Besides these external differences the lower jaw in *Glauconia* is toothed, whereas in *Typhlops* it is edentulous and the teeth are situate on the maxilla.

Text-figure 30.



Pectoral girdle of *Scolotes anguina*.

Text-figure 31.

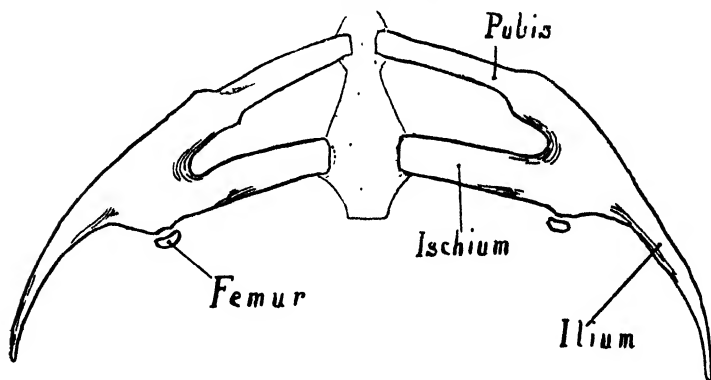


Pectoral girdle of *Scolotes caffer*.

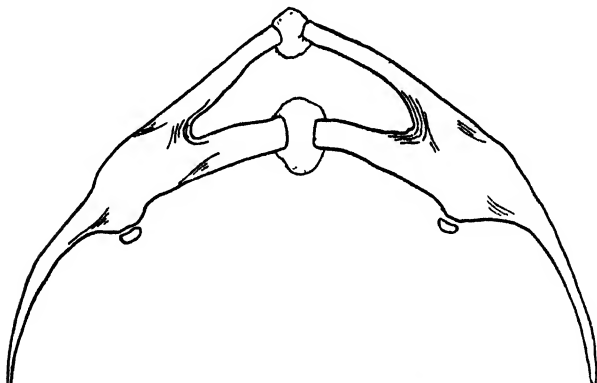
Boulenger (Cat. of Snakes, Brit. Mus. 1893) describes the pelvis as follows:—"Pelvis present, consisting of ilium, pubis, and ischium; the latter forming a symphysis."

Peters figured the girdle of *Glauconia macrolepis*, and his drawing and Boulenger's description tally.

Text-figure 32.



Text figure 33.



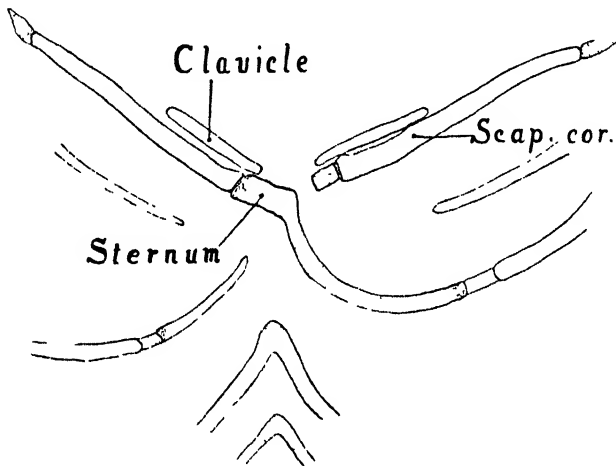
Figs. 32 & 33.—Pelvic girdles of *Scolotes anguina*.

In all three specimens dissected the minute remnant of the femur was present.

For the purpose of this paper, as wide a range of species as possible was studied, and an intensive study was made of one species, viz., *Glauconia nigricans*. Dissections were made of *G. conjuncta*, *G. scutifrons*, *G. nigricans*, *G. albifrons*, *G. gracilior*, and *G. distantii*. Of *G. nigricans* nearly one hundred specimens have been dissected; and, although some very young ones have been caught, it has so far proved impossible to obtain embryological material either in the field or by attempting to breed in captivity.

The main results of the dissections were to show the small amount of variation in the South African species and the remarkable similarity between the girdles of the South African species and the South American *Gluconia macrolepis*, and it has been thought that this tended to show that a degenerate organ may remain, even though it may be functionless, and thus support was claimed for the theory of discontinuous evolution. After dissecting more than one hundred specimens, I am of the opinion that the organ cannot be regarded as functionless and that the fixity is more apparent than real.

Text-figure 34.

Pectoral girdle of *Feylinia currorii*.

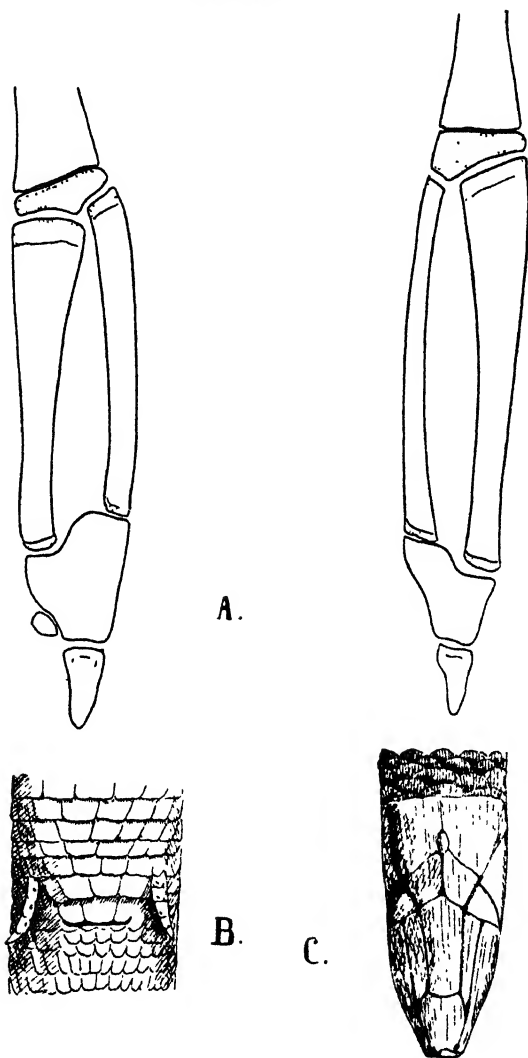
From a specimen kindly presented by the American Museum of Natural History, New York.

It was noticed during dissection that the greatest amount of variation appeared in the size of the claw and its nearness to the skin, and one was led to think that possibly the claw might protrude, even though its protrusion were temporary; and in one specimen there appeared undoubted evidence of this. The tip of the claw protruded through the skin in the fifth row of scales anterior to the cloaca. When the skin was removed the perforation was visible (text-fig. 39, D), and on dissection it was found that one-third of the claw had protruded through the skin. In text-fig. 39, E, the claw appears to turn anteriorly; actually it protrudes downwards and forwards.

The specimen from which this girdle was taken was an adult male with fully-developed testes, and it seemed significant that the specimen which had the best-developed testes should also

have protruding claws. Very little is known of the habits of these animals, but it is remarkable that more males than

Text-figure 35.



A. Hind limbs of *Tetradaotylus africanus*.

B. External view of rudimentary hind limbs.

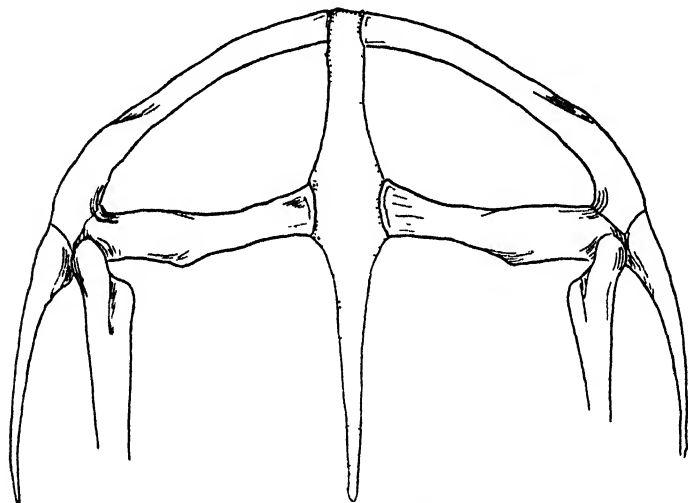
females are captured. They are usually found under stones which cover the mouths of their small burrows. There are

seasons when very few can be found, and I would suggest that those seasons are the breeding-seasons and the animals are then underground.

It is possible that the claw may protrude only at the breeding-season, being used during copulation. If this be so, it will account for very few specimens taken with protruding claws. Moreover, if the claw be protracted after the breeding-season, no trace of a perforation would be seen before the next season, since the old skin would have been cast and a new unperforated one would have taken its place.

Although the South African species possess vestiges which agree in the main with Boulenger's description and with Peters's

Text-figure 36.



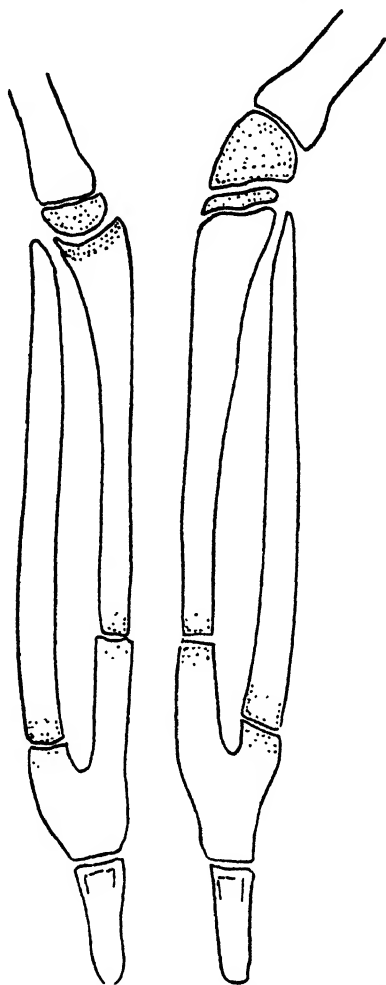
Pelvic girdle of *Tetradactylus africanus*.

figure of *G. macrolepis* from Venezuela, it was found that the girdle of *G. albifrons* (text-figs. 48 & 49) from Tropical America possessed a girdle far more degenerate. Two specimens were dissected, and the girdle was found to be entirely cartilaginous; and it is probable that it represents the fused remnants of the ischia, pubes, and ilia. No trace of a femur was found, and it is beyond doubt that the girdle represents a further stage in the degeneration of the pelvic girdle—in fact, it may be considered as more degenerate than the girdle of *Typhlops delalandii* and almost comparable to that of *Typhlops acutus* from Madras. This being so, it can no longer be held that the girdle of *Glauconia* has reached a fixed stage of degeneration; and, since it has been shown that in *Glauconia nigricans*, at least, the claw

may protrude through the skin, one may consider this girdle as a degenerate organ, probably functional—at present in an evolutionary stage to further reduction rather than as a functionless organ in a fixed stage of degeneration.

Text-fig. 37.

Text-fig. 38.

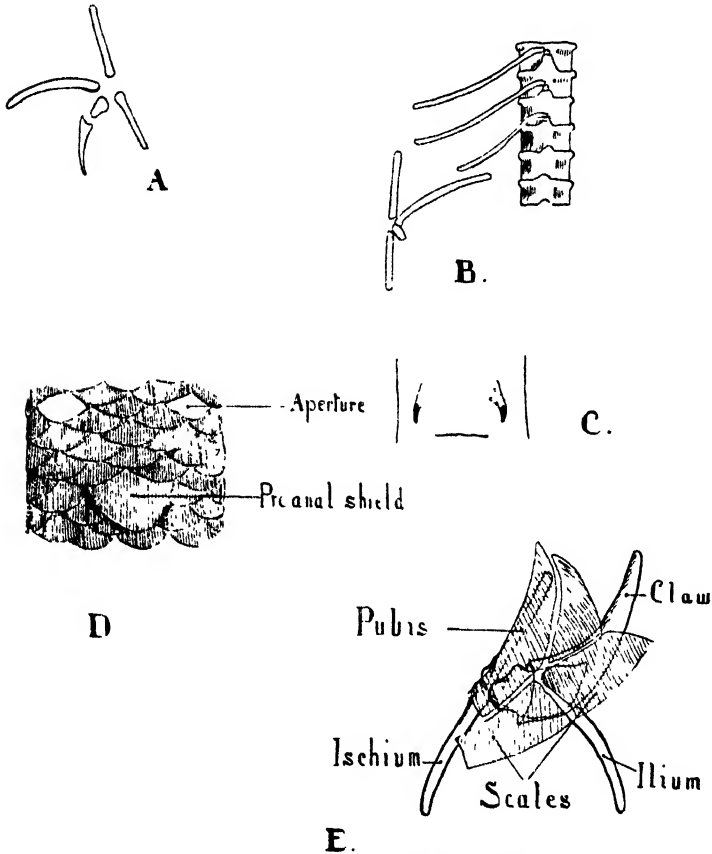
Figs. 37 & 38.—Fore limbs of *Tetradactylus africanus*.

Degeneration in the Pelvic Vestiges of the Snake Typhlops.

The genus *Typhlops* comprises a large number of worm-like burrowing snakes widely distributed in tropical and subtropical

countries. In conformity with the usual custom among burrowing reptiles, whether of the Lacertilia or Ophidia, the tail is extremely short. Gadow* considers them to be "the last

Text-figure 39.



- A. Left leg of pelvic girdle of very young *Glauconia nigricans*.
 B. The position of the girdle in relation to the ribs.
 C. The claws as they appear with the skin removed.
 D. Drawing to show apertures through which the claws protruded.
 E. Position of the claw when protruding. Usually it points backward, but in this case it was pointing downwards and forwards.

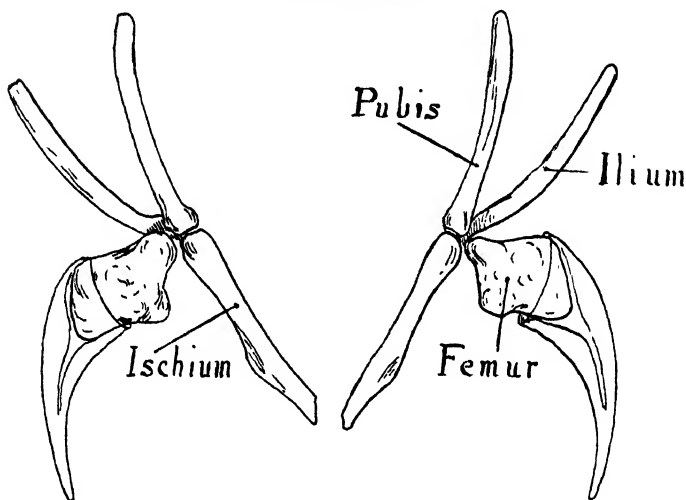
living descendants of formerly cosmopolitan, rather archaic snakes, which in adaptation to their burrowing life and insectivorous diet have undergone degradation."

* 'Amphibia and Reptiles,' Camb. N. H. vol. viii. p. 594.

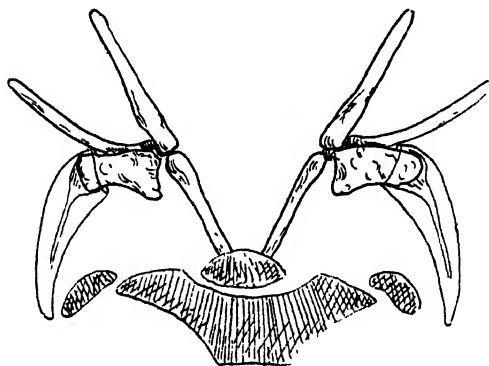
Peters *, in his monograph on the Fauna of Mozambique, figures *T. dinga*, and shows vestiges of a pelvic girdle consisting of two small bones just anterior to the cloacal opening.

For the purpose of this paper two aims were kept in view.

Text-figure 40



Text-figure 41.



Figs. 40 & 41.—Pelvic girdles of *Glaucania nigricans*.

First, to examine the vestiges of species with as wide a geographical range as possible, and, secondly, to make a fairly intensive study of the vestiges in other species.

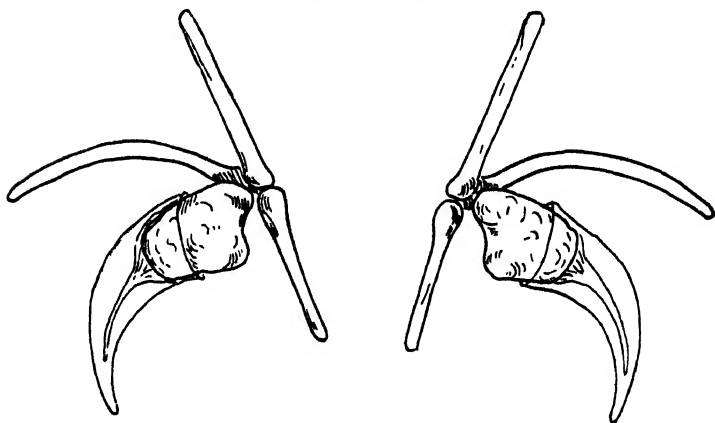
Species have been examined from the West Indies, the Cape Province of South Africa, South-West Protectorate, Rhodesia,

* Peters, 'Reise nach Mossambique,' vol. iii., Berlin, 1882.

Mozambique, Angora, India, and Malay, and a fairly intensive study has been made of *T. delalandii*, from the Cape Province, in order to see what range of variation exists within the species.

T. delalandii (text-figs. 50-61) was first dissected, and it was found to differ from Peters's figure of *T. dinga* in so far as

Text-figure 42.



Text-figure 43.

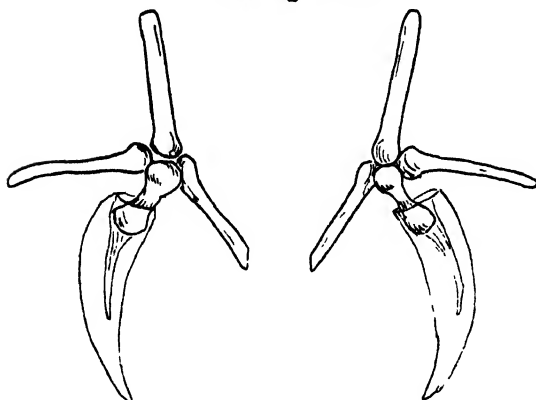


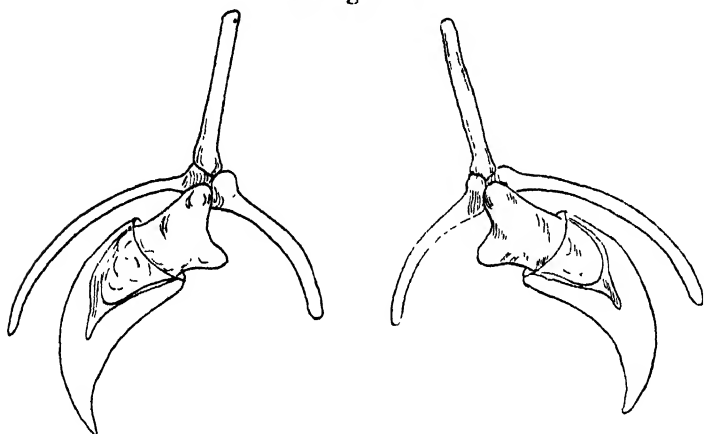
Fig. 42.—Pelvic girdle of *Glauconia conjuncta*.

Fig. 43.—Pelvic girdle of *Glauconia scutifrons*.

it possessed not only the two bones figured by that author but various cartilages. It is fairly reasonable to suppose that the ossified elements represent the *ischia*, while the backwardly pointing cartilages are the *ilia* and the anterior ones the *pubes*, while the posterior cartilaginous appendages of the *ischia* are the *hypoischia*.

There is very little variation within the species, only text-figs. 60 & 61 being anomalous. Text-fig. 61 represents an abnormality which is purely pathological, and hence can be safely disregarded in any consideration of the fixity or otherwise of the regenerative stage of the girdle. The girdle represented in text-fig. 61

Text-figure 44.



Text-figure 45.

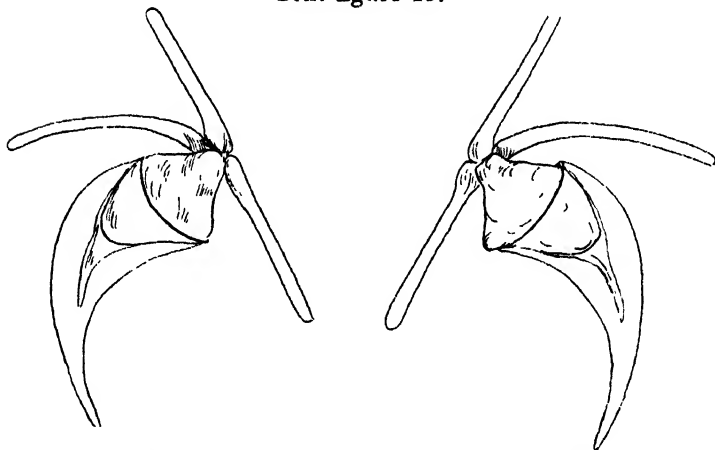


Fig. 44.—Pelvic girdle of *Glauconia conjuncta*, No. 5037 Pretoria Museum. (From Wakkestroon, Transvaal.)

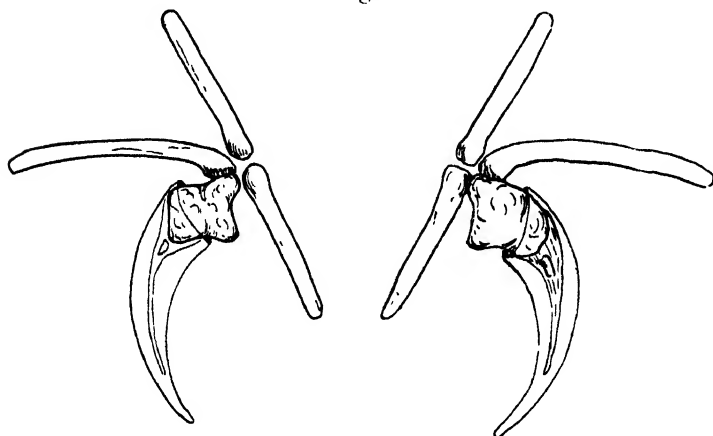
Fig. 45.—Pelvic girdle of *Glauconia gracilior*.

shows a widening at the anterior end of the *ischia*, and the right pubic cartilage is absent. In view of the fact that out of twenty specimens dissected one only showed an unexplainable variation, I am of the opinion that the girdle of *T. delalandii* may be

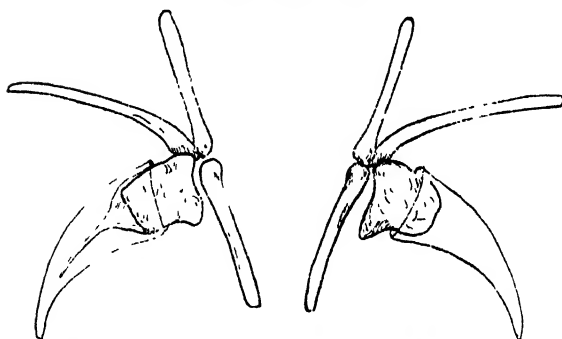
considered as being almost constant in form. In my preliminary work on this species I figured as a girdle of *T. delalandii* a girdle which has been wrongly identified*.

The three girdles of *T. bibronii* (text-figs. 62-64) are fairly constant, each has very pronounced pubic cartilages. Text-fig. 62 represents the girdle of a young specimen, and the meagre ossification may possibly be due to this fact. Text-fig. 65 shows

Text-figure 46



Text-figure 47.



Figs. 46 & 47 — Pelvic girdle of *Glandonia distanti* from Zululand.

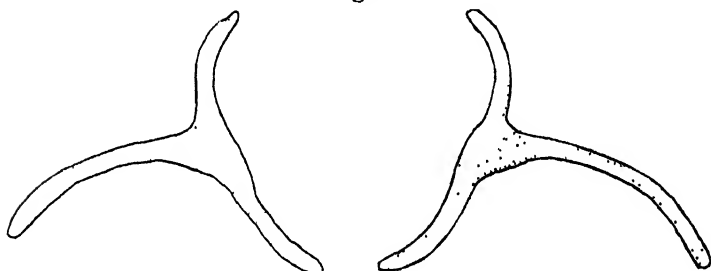
T. schinzi from the South-West Protectorate, which has a distinctive girdle and the pubic cartilages are extremely small. Unfortunately, only one specimen of this species was obtainable; hence it is impossible to judge of the fixity or otherwise of this type. *T. lumbricalis* (text-figs. 66, 67, & 68) from the West Indies shows rather less degeneration than *T. schinzi*. I regard

* Duerden and Essex, S.A. Journal Nat. Hist. vol. iv. No. 3, p. 176. Fig. 5 should be *T. mucroso*, not *T. delalandii*.

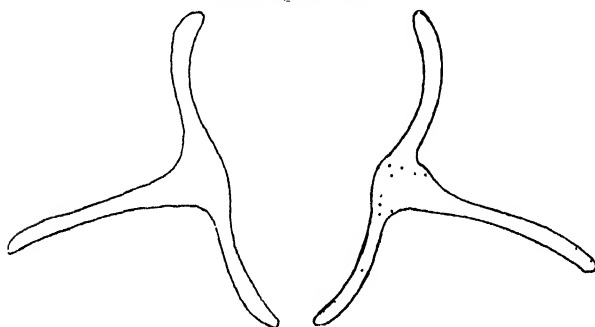
the widening of the tips of the pubes as purely incidental, and would regard the girdle here as distinctive of the species.

T. mucroso (text-figs. 71-74), from Rhodesia, is still more degenerate. In one only of the specimens examined is there a distinct pubic cartilage. This girdle is otherwise abnormal, since there is an ossification of the ilium; and since this peculiarity appeared once among the fifty specimens examined, one may explain it as an atavistic mutation and hence not typical of the species. *T. schlegeli* (text-figs. 69 & 70), also from Rhodesia, shows marked similarity to *T. mucroso*, although I would

Text-figure 48.



Text-figure 49.

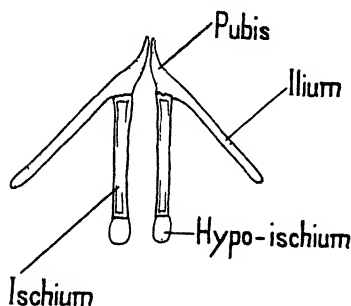


Figs. 48 & 49.—Pelvic girdle of *Glauconia albifrons* from Venezuela.

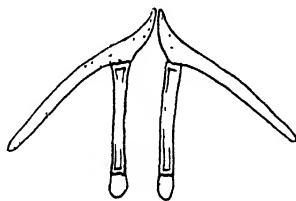
consider *T. schlegeli* as having a more degenerate girdle, owing to the complete absence of any indication of the pubes. *T. acutus*, from Madras (text-figs. 75 & 76), has, in the two specimens examined, an entirely cartilaginous girdle; and, although the ilia and pubes are present, I would therefore consider this girdle as possibly more degraded than that of *T. schlegeli*. In *T. nigroalbus* (text-figs. 79 & 80), from Penang, the ilia and pubes are extremely small, even though one be prepared to regard the cartilaginous knobs at the anterior ends of the *ischia* as the remnants of these bones. *T. vermicularis*, from Angora,

(text-figs. 81 & 82) is still more degenerate, and *T. braminus* (text-figs. 83 & 84) has merely two very thin *ischia* with small cartilages at either end. A third specimen shows two cartilaginous rods only. *T. mossambicus* (text-figs. 77 & 78) from Lourenço Marques has a girdle still more degenerate, since the amount of ossification is very small, being only 3 mm. long.

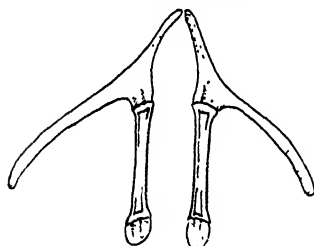
Text-fig. 50.



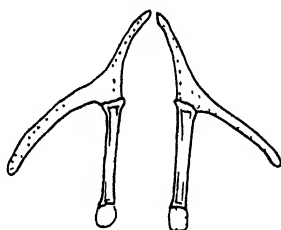
Text-fig. 51.



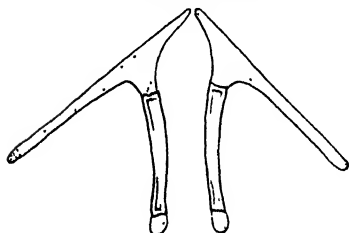
Text-fig. 52.



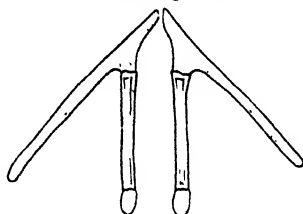
Text-fig. 53.



Text-fig. 54.



Text-fig. 55.



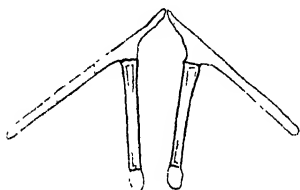
Figs. 50-55.—Pelvic girdles of *Typhlops delalandii* from Eastern Province, S.A.

Anomalepis mexicana was also dissected. This snake was placed by Boulenger (Cat. Rep. B.M. p. 59) among the Glauconidæ. Emmett Dunn placed it in the Typhlopidae. On dissection I found no trace of a girdle. Emmett Dunn*, suggested the placing of *Anomalepis mexicana* in the Typhlopidae.

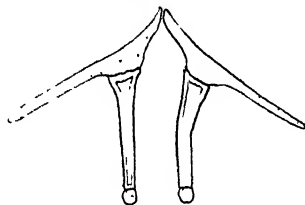
* Proc. Biol. Soc. of Washington, vol. xxxvi. 1923.

mainly because the teeth were found to be on the maxilla as in *Typhlops* and not on the dentary as in *Glauconia*; but *Anomalepis* and *Glauconia* have enlarged preanal shields, while *Typhlops* has normal ones. Moreover, the head-shields of *Anomalepis* are almost typically Colubrid. It is therefore doubtful whether Emmett Dunn is correct in placing *Anomalepis* in the Typhlopidae, although he is certainly justified, from the position of the teeth, in removing it from the Glauconidae. (Moreover,

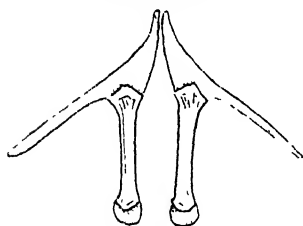
Text-fig. 56.



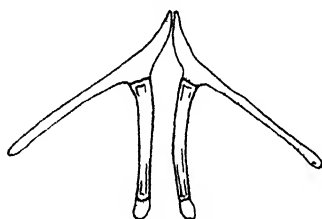
Text-fig. 57.



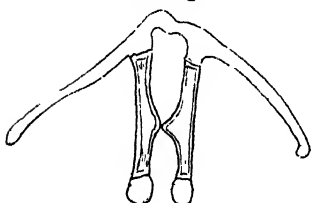
Text-fig. 58.



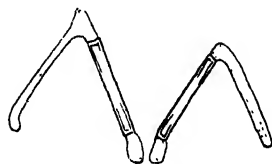
Text-fig. 59.



Text-fig. 60.



Text-fig. 61.



Figs. 56-61.—Pelvic girdles of *Typhlops delalandii* from Eastern Province, S.A.

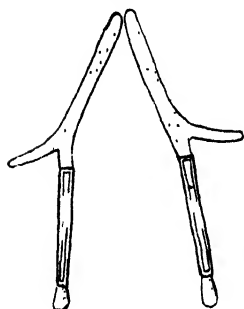
the Glauconidae have always a well-developed pelvic girdle possessing pubes, ilia, ischia, and femur, and in the absence of this well-defined girdle the removal from the Glauconidae becomes more justified.) The absence of any pelvic vestiges does not provide an insurmountable obstacle to its inclusion in the Typhlopidae, since it has been shown that *Typhlops* may possess a fairly well-defined girdle as in *T. delalandii* or varying types of girdles down to the minutest cartilaginous rods as in *T. braminus*, and hence *Anomalepis* might

possibly be looked on as a member of the Typhlopidae possessing no remnant of a pelvic girdle. Nevertheless, I would not be prepared to consider it as otherwise than an anomalous member of the family because of its undoubted Colubrid head-shields.

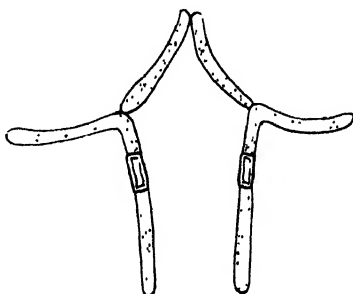
A study of the girdle-vestiges of *Typhlops* makes its clear that this character may be regarded as distinctly specific.

It is noteworthy that the northern and eastern forms—i. e.,

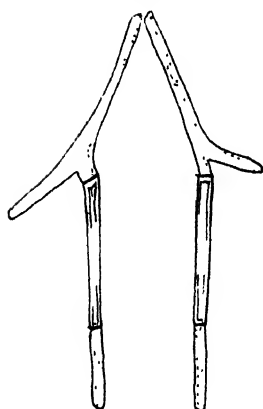
Text-fig. 62.



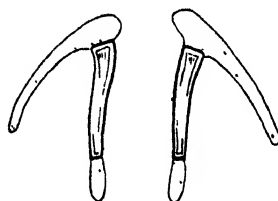
Text-fig. 63.



Text-fig. 64.



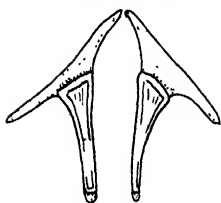
Text-fig. 65.



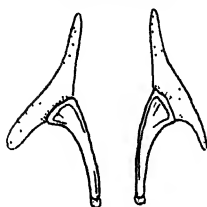
Figs. 62, 63, 64.—Pelvic girdle of *Typhlops bibronii* from Eastern Province, S.A.
Fig. 65.—Pelvic girdle of *Typhlops schinzi* from South-West Protectorate.

from Mozambique, Angora, and India—are the most degenerate, and of the species examined *T. delalandii* from Cape Colony is the least degenerate. It would thus seem that *T. delalandii* is the most primitive, and left the centre of dispersal apparently situated in Northern Africa and Asia Minor, first, and the succeeding evolutionary waves are represented by *T. bibronii*, *T. mucruso*, *T. schlegeli*, etc., approximately in the order named. How *T. lumbricalis* reached the West Indies is debatable, but

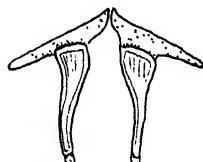
Text-fig. 66.



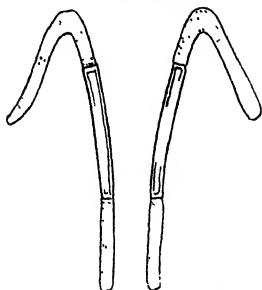
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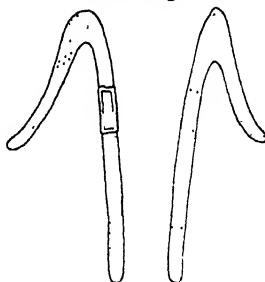
Text-fig. 68.



Text-fig. 69.

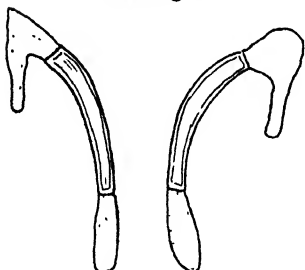


Text-fig. 70.

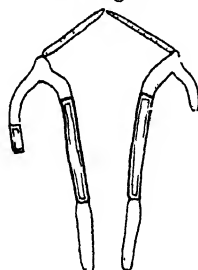


Figs. 66 & 67.—Pelvic girdles of *Typhlops lumbricalis* from St. Thomas.
 Fig. 68.—Pelvic girdle of *Typhlops intermedius (lumbricalis)* from West Indies.
 Figs. 69 & 70.—Pelvic girdle of *Typhlops schlegelii* from Rhodesia.

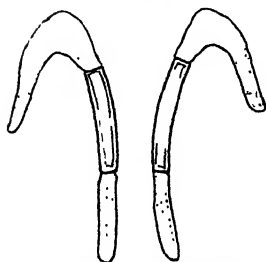
Text-fig. 71.



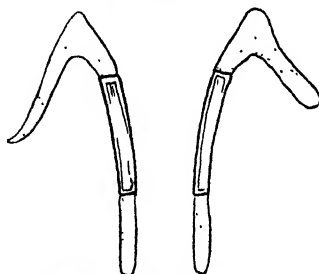
Text-fig. 72.



Text-fig. 73



Text-fig. 74.

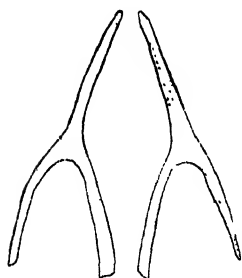


Figs. 71-74.—Pelvic girdles of *Typhlops mucruso* from Rhodesia.

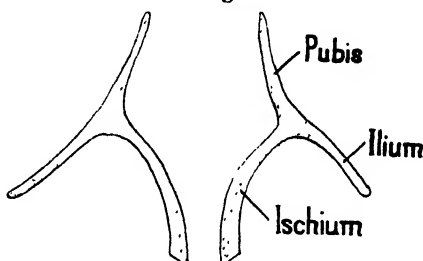
if the above hypothesis be held, *lumbricalis* must represent a stage reached quite early in the dominant period of *Typhlops*.

In view of the facts that species found in different countries have girdle-vestiges varying in their degrees of degeneration, and also that the constituent parts of the girdle tend to vanish by small degrees, it is fairly reasonable to suppose that the text-figs. 58-86 represent probable stages of descent. Such a series when found within a genus is more likely to be truly representative of the stages of descent than when

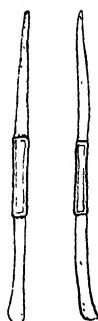
Text-fig. 75.



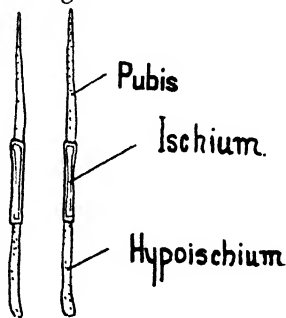
Text-fig. 76.



Text-fig. 77.



Text-fig. 78.

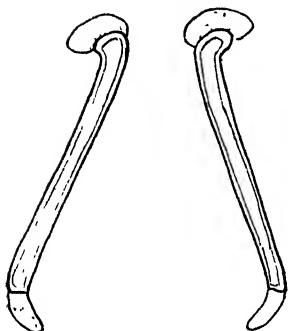


Figs. 75 & 76.—Pelvic girdles of *Typhlops acutus* from Madras.

Figs. 77 & 78.—Pelvic girdles of *Typhlops mossambicus* from Lourenço Marques.

found within a species as in *Chamaesaura anguina*, since if the series be found within the species it pre-supposes a very rapid evolution of the final stage. Moreover, the series when found within the species is more likely to be a factitious one due to intermingling which would not happen within a genus. Although this consideration detracts from the value of the series within a species, it by no means makes it worthless, and one is bound to agree with Kreig (1919), who, after measuring the intensity of variation in degenerate forms of lizards and comparing it with the intensity of variation in related normal

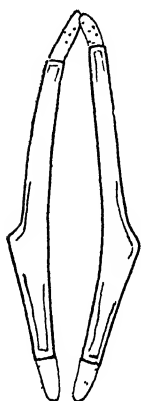
Text-fig. 79.



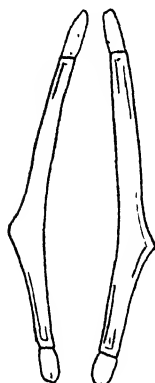
Text-fig. 80.



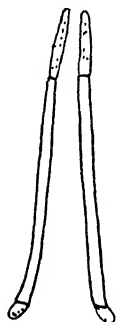
Text-fig. 81.



Text-fig. 82.



Text-fig. 83.



Text-fig. 84.



Figs. 79 & 80.—Pelvic girdles of *Typhlops nigroalbus* from Penang.

Figs. 81 & 82.—Pelvic girdles of *Typhlops vermicularis* from Angora.

Figs. 83 & 84.—Pelvic girdles of *Typhlops braminus* from Godavery Valley, India.

forms, came to the conclusion that marked variation is a symptom of degeneration, although it does not follow that it is *a sine qua non*.

The fact that *T. braminus* (text-figs. 83 & 84), which has a very degenerate girdle, should also be found in South Africa does not detract from the theory of the eastern origin, since, although there are found in the south very degenerate (*i.e.*, highly specialized) types, like *T. braminus*, and less degenerate (*i.e.*, less specialized) types like *T. delalandii*, the eastern forms have on the whole much more degenerate girdles than the African species, and, moreover, the more highly specialized types (*T. braminus*, *T. vermicularis*) have a wider distribution and encroach on the countries inhabited by the older (less degenerate) species, whereas the reverse does not take place — *e.g.*, *T. braminus* is found in the whole of Southern Asia, the islands of the Indian Ocean, and Africa, south of the Equator, whereas *T. delalandii* is found only in South Africa.

*The Geographical Distribution of Lizards in South Africa,
with special reference to Primitive and Degenerate Forms.*

Any consideration of the geographical distribution of reptiles in South Africa necessitates a study of the geography and to a lesser degree the geology of the country. The main geographical feature is the watershed which runs from Ceres in the Western Province and proceeds in a general east-north-east direction for one thousand five hundred miles. It is formed by various ranges, *viz.*:—the Klein Roggeveld, N. Nieuwveld, Stormberg, and the Drakensberg. To the north of this range the land slopes gradually to the Orange River. Between the watershed and the sea on the south are several ranges, and between the ranges is a series of plateaux which decrease in altitude step by step until they reach the Indian Ocean. The heights of the watershed vary from 5000 to 11,500 feet, the culmination being reached at the Mont-aux-Sources in the Drakensberg.

The western portion of this watershed is composed of sedimentary rocks belonging to either the Cape or the Karroo system. The Karroo beds have a maximum thickness of 15,000 feet, and it is remarkable that there is no evidence pointing to the fact that marine conditions prevailed at any time during its deposition.

The Beaufort beds form the middle of the series, and from them a very varied and extremely interesting series of fossil reptiles has been described by Seeley, Broom, Owen, Huxley, and Cope. The highest parts of the watershed are composed of Drakensberg Volcanics, which are the uppermost beds of the Karroo system. These beds have a vertical thickness at Mont-aux-Sources of 4500 feet.

The Eastern portion of the Cape Province, Natal, Basuto Land,

and the Orange Free State get summer rains, while the Western Province has winter rains. Although many parts of the Eastern Province have an average rainfall of 22" or more, there are times when these parts look little else than deserts, owing to the fact that the rain is not evenly distributed throughout the season, but falls as very heavy storms followed by long periods of drought. This unequal distribution of rainfall accounts for the fact that many South African plants are xerophytic.

Zoological Areas.

It is often assumed that there is some degree of correlation between the distribution of plants and of animals, and that both are determined by geological and climatic factors. There is undoubtedly an element of truth in this assumption, but I am convinced that geological factors have, in South Africa, a comparatively small share in determining the limits of any species or genus. Further, I am convinced that it is impossible to divide South Africa into faunal regions comparable with the floral regions of Engler and others. Sharply-defined zoological areas can only be found when such areas are bounded by physical barriers which are insurmountable. In South Africa there are no such barriers, and hence no sharply-defined zoological areas. It is remarkable that where such areas do exist their faunas seem to be aggregations of heterogeneous units which have become isolated in these areas, and hence are of little value in the consideration of ecological problems.

Although South Africa possesses no insurmountable barrier, it possesses two partial barriers which have influenced the trend of the waves of invasion. These two are the Limpopo River and the watershed previously mentioned.

The author was, first, impressed with the fact that it was impossible to divide South Africa into zoological areas, and, secondly, with the fact that in any study of the zoogeography of the country it was essential to examine the watershed along its entire length, and, further, it was necessary to examine the coastal belt between the watershed and the sea, and then to examine the land to the north.

This work had to be commenced *de novo* because the records which were in existence were very meagre and contained no points of any ecological value. For example, Smith records *Lygosoma sundevalli* "in the country, to the eastward of Cape Colony," and he records *Scelotes caffer* from "most parts of Southern Africa: found under stones or in loose soil near the roots of shrubs." One might infer from the above that *Scelotes caffer* was reasonably common, yet in the course of expeditions aggregating 20,000 miles I have found *Scelotes caffer* once.

Expeditions undertaken.

The sketch-map (Pl. III.) shows the routes undertaken by the author in his attempt to examine the watershed and the plains on

either side of it. Every route has been travelled twice and some many times, and, although the examination has not been complete and could probably never be complete, it is hoped that the data collected and the conclusions arrived at may be found of use. The total distance travelled was twenty thousand miles and the following is the schedule adopted. First, an intensive examination of the Grahamstown area was made, and here 668 specimens belonging to 20 species were collected; the range of trips was gradually widened until the author had acquired a fair knowledge of the oecology of the reptiles of the Albany district.

Then various longer expeditions were organized.

1. Across the Karroo to Graaf Reinet; south of the Zuurberg, along the Little Karroo Oudtshoorn, through the Outeniqua Mountains to the coast, along the coast near Zitzikamma Mts. to Port Elizabeth and then to Grahamstown.

2. To the Amatola Mountains.

3. Along the coast-belt to Cape Town, with various excursions into the mountains.

4. Across the Great Winterberg.

5. To the Stormberg Range near Queenstown and to Tembuland.

6. Across the Katberg Range.

7. To the Stormberg, Orange Free State, across the Drakensberg at van Reenan's Pass, through Natal, Griqualand, and the Transkei.

8. Across the Katberg to the Stormberg, the Transkei, Natal, to the southern slopes of Mont-aux-Sources, to the summit of Mont-aux-Sources from the northern side, returning *via* the Orange Free State across the Stormberg at Middelberg.

9. Across the Karroo to the Swartberg, returning through the Outeniqua Mountains to Grahamstown.

The following are the records of species taken during the expeditions. New species discovered are marked with an asterisk:—

FAMILY GECKONIDÆ.

PACHYDACTYLUS MACULATUS Gray.

Amatola Mountains, Fort Beaufort, Grahamstown, Port Elizabeth, Hermanus.

This Gecko is fairly common in the Eastern Province, and is usually found under stones, often in conjunction with *Zonurus cordylus* or with the Scorpions. There is a common but erroneous opinion that it is poisonous. It is a timid and rather friendly lizard and can easily be kept in captivity when provided with small insects. It is oviparous, and the eggs are usually laid in pairs, although on one occasion I found a cluster of thirteen eggs. These eggs hatched out three weeks after being collected. The young average 20 mm. in length, are blackish in colour, and the

tail is quite thin. When captured the adult has a habit of losing its tail, and the regenerated tail is much wider than the original one. Also when caught it often emits a distinct squeak.

PHYLLODACTYLUS PORPHYREUS Daud.

Cape Peninsula (Kirstenbosch and Constantia).

This Gecko is much larger than the preceding one, and may reach the length of 100 mm. The young are dark brown with long reddish tails, and when hatched measure 30 mm. The adults are greyish with dark brown variegations above and a grey stripe down the centre of the back from the neck to the base of the tail. They are much more active than *Pachydactylus maculatus*.

PACHYDACTYLUS CAPENSIS Smith.

Tarkastad, Mont-aux-Sources.

PACHYDACTYLUS BIBRONI Smith.

Hounslow, near Grahamstown.

LYGODACTYLUS CAPENSIS Smith.

Pietermaritzburg.

EDURA NIVARIA Boul.

Stormberg Range, near Cala.

EDURA TEMBULICU * Hewitt.

Cofimvaba and Southern Tembuland.

EDURA KARROICA Hewitt.

Graaf Reinet.

EDURA KARROICA var. *WILMOTI* Hewitt.

Tarkastad.

EDURA *, sp. n.

South slopes of Mont-aux-Sources.

On Jan. 2nd, 1925, I collected twenty-four eggs of *P. porphyreus* at Constantia in the Cape Peninsula. There were thirteen in one cluster, eight in another, and three in the other. During the ensuing motor journey of one thousand and more miles seven were broken. On February 5th seven hatched out and a few days later six others. The young were at first covered with a thin transparent membrane. This vanished shortly, and, judging from the fact that I found no trace of it, it is highly probable that it constitutes the young gecko's first meal.

PHYLLODACTYLUS ESSEXI * Hewitt.

Hounslow (ten miles north of Grahamstown).

The adult of this species has a superficial resemblance to the young of *P. porphyreus*. It was found on a rocky hill, and on the same hill I have taken *Zonurus cordylus*, *Eremias pulchella*, *Mabuia varia*, *Acontias meleagris*, and *Typhlops delalandii*.

CEURA AMATOLICA * Hewitt.

Hogsback on the Amatola Mountains and Katherg Range.

Three specimens were found under stones at a height of about six thousand feet. In this neighbourhood, where I collected very carefully, no trace of *Pachydactylus* or *Phyllodactylus* was found.

Family AGAMIDÆ.

AGAMA ATRA Daud.

Amatola Mountains, Fort Beaufort, Grahamstown, Port Alfred, Port Elizabeth (Schoenmaker's Kop), Hermanus, Houw Hoek, Sir Lowry's Pass, Cape Peninsula, Bains Kloof, Tradows Pass, and Mossel Bay.

This Lizard has a very wide distribution. It can be found on the sea-shore, on the Karroo, and on the tops of mountains. On the sea-shore at Hermanus I have found it in fairly large numbers on rocks which are covered at high tide. In the breeding-season the head of the male becomes a vivid blue. It always inhabits the neighbourhood of large stones, and is extremely difficult to catch, owing to its quickness and to its power of jumping. I have seen an adult *Agama* jump to a height of twelve inches and land on the perpendicular face of a rock; and I have seen another adult when hard pressed leap with its legs and toes outstretched to a point on another rock two feet lower and three feet away from the point where it was standing. These lizards usually bask in the sun, and they have a quaint habit of raising and lowering the head and shoulders, at the same time turning the head from side to side. They watch intently anything approaching from the front, and if one attracts their attention in this manner a second person can often easily capture them from the rear.

Family ZONURIDÆ.

ZONURUS CORDYLUS Linn.

Hogsback (Amatola Mountains), Gaika's Kop (Amatola Mountains), Mitchel's Pass (*Seymour*), Fort Beaufort, Port Alfred, Port Elizabeth, Hermanus, Houw Hoek, Hottentots Holland Mountains, Sir Lowry's Pass, Cape Peninsula, Bains Kloof, Montagu.

This is probably the commonest Lizard in the coastal districts of Cape Province. I have taken it from the sea-shore to Gaika's Kop at a height of 6,000 feet. It also seems to be the hardest.

Lizards are usually considered to be almost entirely insectivorous; on one occasion I saw *Z. cordylus* attack and eat a small skink. It lives in narrow cracks between rocks, and, owing to its dorsi-ventral flattening, it can squeeze into very narrow clefts and is hard to dislodge. At Hermanus *Zonurus* appears to have departed somewhat from its rupicolous habits, and there often lives in holes in the earth after the manner of *Gerrhosaurus flavigularis*. While collecting on a trip from Grahamstown to Capetown, I noticed that specimens taken in the Eastern Province and the south-eastern districts were all reddish with yellow variegations. At Hermanus most of the specimens had black heads, and as one proceeded westwards they became blacker, until in the neighbourhood of Capetown most of the specimens taken were entirely black. It is possible that on a closer examination it may be found that there are two or several varieties.

PSEUDOCORDYLUS MICROLEPIDOTUS Smith.

Amatola Mountains, Grahamstown, Tembuland, Drakensberg Range.

On the Mont-aux-Sources it was found on the summit in large numbers. At Hogsback I twice observed this species in the act of feeding on a rock-encrusted lichen.

ZONURUS CÆRULEO-PUNCTATUS Hewitt & Methuen.

This species somewhat resembles *Z. cordylus*, but is slenderer and marked with bright blue spots—it is deep yellow ventrally. I found it living in the wall on the Montagu Pass in the Outeniqua Mountains. It basks in the sun, but is extremely hard to catch. In a distance of a mile along the wall I counted thirty specimens of *Zonurus cæruleo-punctatus* (of which three were captured), one *Tropidosaura montana*, and one *Mabuia varia*.

CHAMESAURA ANGUINA Linn.

Coldspring (six miles west of Grahamstown), Woest Hill (four miles south-east of Grahamstown), Bains Kloof, Cape Peninsula.

This serpentiform lizard has minute remnants of limbs and a very elongated tail. Most of the surface-frequenting serpentiform lizards usually live in grassy country, but of the five specimens of *C. anguina* I have taken two were in rocky country. The Bains Kloof specimen was gliding over the flat surface of a large rock, and its motion was so snake-like that at first I mistook it for a specimen of *Psammophis crucifer*.

I have watched these lizards for any sign of limb-movement, and so far have not been able to detect any. There is a distinct difference between the movement of the surface-frequenting serpentiform lizards and the burrowing serpentiform types. The former are typically snake-like and particularly graceful in their movements. The short-tailed burrowing forms, such as *Acontias*, move jerkily with a lateral whip-like movement.

Family GERRHOSAURIDÆ.

GERRHOSAURUS FLAVIGULARIS Wiegman.

Grahamstown, Bath's Hill (eight miles north-east of Grahamstown, Port Elizabeth (Schoenmaker's Kop), Hermanus.

At Port Elizabeth and Hermanus *G. flavigularis* was found on the shore living in holes under bushes in close proximity to *Zonurus cordylus*, *Mabuia varia*, and *Mabuia homalocephala*.

G. flavigularis has a yellow throat and a narrow but very distinct band arising above the posterior corner of the eye and running the length of the body. The sides, especially of the neck, are barred with black and yellow, and the back is variegated with black markings and small yellow dots. *G. flavigularis* is distinctly untamable and attempts to bite whenever possible. Crickets seem to be the favourite food, as I have ascertained by actual dissections.

TETRADACTYLUS SEPS Linn.

Cape Peninsula.

This Lizard has a deep olive-bronze colour on the back and ventrally a metallic iridescence. The upper lip has yellow spots, not quite so plainly marked as in *Tetradactylus tetradactylus*, where the markings are continued along the neck. It lives under stones, and appears from its proportions to be in the first stages of serpentiform degeneration.

TETRADACTYLUS LEVICAUDA Hewitt.

Amatola Mountains and Katberg Range, 6000 feet.

This species is very similar in coloration and also in habit to *T. seps*, but the tail is proportionally longer.

TETRADACTYLUS TETRADACTYLUS Lacép.

Cape Peninsula.

T. tetradactylus resembles in proportion and habit *Chamaesaura anguina*, except that in *C. anguina* degeneration has proceeded much further, and whereas in *Chamaesaura* the limbs do not appear to be in use, in *T. tetradactylus* they are used to a certain extent. For the most part the animal glides along with a serpentiform movement, but when at rest it sometimes raises itself from the ground by means of its limbs. It is impossible to say whether the limbs move as it glides along, since the rate of progress is too rapid.

Family SCINCIDÆ.

MABUIA TRIVITTATA Cuvier.

Amatola Mountains, Fort Beaufort, Grahamstown, Port Elizabeth, Hermanus, George, Mossel Bay, Caledon, Cape Peninsula, and Umtata.

This Lizard is fairly common over a wide area, and I have rarely found it far away from houses. I have found it living on garden rockeries, in holes in the trunks of trees, and under bushes. When fully grown it has rather a heavy body and is by no means as agile as the Lacertids. On the Amatola Mountains it was taken near to the Hogsback Hotel.

MABUIA HOMALOCEPHALA Wiegman.

Grahamstown, Hermanus, Cape Peninsula.

This species and *M. varia* are very similar in general appearance. Each has a lateral streak passing through the ear, but in *H. homalcephala* this streak is often yellow and is edged inferiorly with a dark band which is again edged with a whitish band; also in *H. homalcephala* the hind limb will barely meet the adpressed fore-limb, whereas in *M. varia* it invariably covers the hand and often more. There is also a difference of habitat, for *M. varia* lives under bushes, whereas *M. homalcephala* is entirely rock-frequenting.

MABUIA VARIA Peters.

Grahamstown, Port Elizabeth, Hermanus, Cape Elizabeth.

MABUIA STRIATA Pet.

Orange Free State, Drakensberg, Transkei.

MABUIA SULCATA Pet.

Graaf Reinet, Middelberg, Craddock.

ACONTIAS MELEAGRIS L.

Grahamstown, Port Elizabeth, Hermanus.

ACONTIAS GRACILICAUDA * Essex.

Grahamstown.

ACONTIAS BREVICEPS * Essex.

Amatola Mountains.

SCELOTES BIPES Linn.

Cape Peninsula.

The fore limbs are entirely absent, and as the animal moves the small hind limbs are kept close to the body; it is found burrowing in loose earth and has a more snake-like movement than *Acontias* mainly owing to its longer tail.

Family LACERTIDÆ.

TROPIDOSAURA MONTANA Dum. & Bibr.

Amatola Mountains, Grahamstown, Montagu Pass in the Outeniqua Mountains.

Found only on rocky hills and mountains. On the summit of Signal Hill, near Grahamstown, this is apparently the only lizard and is fairly plentiful. As one proceeds lower down the same ridge other species—such as *Pseudocordylus microlepidotus*, *Zonurus cordylus*, *Eremias burchelli*, *Acontias meleagris*—appear; at this lower elevation *Eremias burchelli* becomes plentiful, whilst *Tropidosaura* completely vanishes, but on ascending the next spur of the Zuurberg *Tropidosaura* again appears.

On the Amatola Mountains the same sequence did not hold good, since I found *Tropidosaura* in close proximity to most of the species mentioned previously, while in the Montagu Pass it shared a wall with *Zonurus ceruleo-punctatus*.

Boulenger says of the coloration: "Olive-brown above with two dark and two light longitudinal streaks on either side." To this might be added: the light streaks in the breeding-season become series of yellow dots

TROPIDOSAURA ESSEXI * Hewitt.

Found at the summit of Mont-aux-Sources, 11,500 feet.

NUCRAS DELALANDII M.-Edw.

Sugarloaf Hill, Grahamstown. Only taken once.

NUCRAS TESSELLATA TENIOLATA Smith.

Longford Grange, on the Bushman's River, 30 miles south of Grahamstown.

The coloration is somewhat similar to that of *Eremias burchelli*, with the exception that the tail in the adult of *Nucras* is red for some distance from the tip, whereas in *Eremias* the young only have red tails. Found in a bush near to the river.

EREMIAS BURCHELLI D. & B.

Grahamstown. At various places on the range of hills to the south and west of the town. The favourite habitat is ground dotted with loose stones. It is extremely quick and very hard to catch. Sometimes it is very plentiful, and I have captured eight in less than an hour. One nearly always finds *Trimerorhinus rhombeatus* in the same small locality, and it seems as though this snake is one of the natural enemies of *Eremias*.

EREMIAS LINEOCELLATA PULCHELLA Gray.

Hounsloew (ten miles north of Grahamstown), Avontuur, Riversdale.

Frequents sandy stretches with some stones. It is probably the quickest of all the small lizards.

SCAPTEIRA KNOXI M.-Edw.

Cape Flats. Frequents the extensive sandy wastes to the east of the Cape Peninsula.

The intensive study of the Grahamstown area yielded the following results:—

<i>Pachydactylus maculatus</i>	82
<i>Agama atra</i>	62
<i>Zonurus cordylus</i>	108
<i>Pseudocordylus microlepidotus</i>	8
<i>Chamaesaura anguina</i>	2
<i>Varana niloticus</i>	2
<i>Eremias burchelli</i>	41
<i>Eremias pulchella</i>	1
<i>Nucras delalandii</i>	2
<i>Nucras tessellata tæniolata</i>	7
<i>Tropidosaura montana</i>	27
<i>Mabuia varia</i>	14
<i>Mabuia trivittata</i>	45
<i>Mabuia homalocephala</i>	16
<i>Acontias meleagris</i>	83
<i>Acontias gracilicauda</i>	5
<i>Gerrhosaurus flavigularis</i>	26
<i>Glauconia nigricans</i>	103
<i>Typhlops delalandii</i>	7
<i>Lophosaura ventralis</i>	37
	<hr/>
	678

It will be noticed that the list contains 15 genera and 20 species, of which 4 genera and 5 species are "degenerate," but of the 678 specimens collected 83 belong to one degenerate form and 103 to another. Besides the degenerate lizards I have listed *Typhlops* and *Glauconia*, since they possess remnants of limb-girdles and in their habits are not unlike *Acontias*.

These numbers become significant when compared with the numbers recorded on an expedition where no real intensive work is possible. Tembuland expedition gave the following results:—

<i>Edura tembulica</i>	21
<i>Pachydactylus maculatus</i>	6
<i>Pseudocordylus microlepidotus</i> ..	10
<i>Eremias burchelli</i>	7
<i>Nucras delalandii</i>	2
<i>Mabuia trivittata</i>	2
<i>Mabuia homalocephala</i>	8
<i>Zonurus cordylus</i>	8
<i>Agama atra</i>	7
<i>Glauconia conjuncta</i>	2

It will be noticed that *Acontias* does not appear and that *Glauconia* appears only twice.

During the course of a long trip to Capetown, in which 2000 miles were covered, *Acontias* was taken three times, while neither *Glauconia* nor *Typhlops* was taken.

It would therefore appear at first sight that *Acontias meleagris* is more common in the Grahamstown area than in other parts of the Cape Province, yet an examination of the 46 specimens in the South African Museum shows only one (No. 1075) as having come from Grahamstown. The true reading of these facts is probably as follows:—*Acontias meleagris* is a burrowing limbless lizard and is rarely seen in the open, and hence rarely taken by the casual collector, and much museum material is provided by this type of collector. But if one finds an "*Acontias*" locality and knows its type of hiding-place, it may be taken in fair quantities, and I have little doubt that other districts would yield good results if intensive collecting were done in them.

Reptile Sanctuaries.

Before proceeding to examine in detail the distribution of various species, it is advisable to remark upon and attempt to explain the apparently unwarranted abundance of reptile life in certain very small areas. These areas are rarely more than a few hundred square yards in area, and possess not only a large number of reptiles but also a greater variety of species and genera than is usually found. Such areas seem to deserve the name of Reptile Sanctuaries, and I have chosen one for a detailed description. This particular spot is shown on Pl. VII. fig. 2, and is a small hill on the farm Hounslow, about ten miles north of Grahamstown. The rocks are sandstones of the Witteberg series, and on the northern side they form a small precipice or "krantz," while on the southern slope the whole area measures about one hundred yards by fifty yards. The vegetation is practically all xerophytic in character, and includes the following:—

Mimosa shrubs.

Prickly pears (cactus).

Aloes of various species.

Carissa and *Pachypodium* (*Apocynæ*).

Pelargonium cuculatum and other members of the Geraniaceæ, which are bulbous.

Mesembryanthemums (*Mesembriaceæ*).

Euphorbia resinifera.

Senecio and other xerophytic composites.

Polygala.

Crassulas and Cotyledons.

Morea (*Iridaceæ*).

Hypoxis and *Brunsvigia* (*Amaryllidaceæ*).

Lelago (*Lelagineæ*).

Haleria (*Scrophulariaceæ*).

Grewia (*Tiliaceæ*).

Mistletoe and various lichens.

From this small area with a semi-Karoo flora I have taken the following:—

<i>Pachydactylus hiberni</i>	3
<i>Phyllodactylus essexi</i>	28
<i>Zonurus cordylus</i>	18
<i>Mabuia varia</i>	16
<i>Mabuia homalocephala</i>	6
<i>Acontias meleagris</i>	3
<i>Scelotes caffer</i>	3
<i>Eremias lineocellata pulchella</i>	2
<i>Typhlops delalandii</i>	2
<i>Glauconia nigricans</i>	4
<i>Philothamnus semivariegatus</i>	2
<i>Homopus areolatus</i>	2
<i>Testudo angulata</i>	2

Of the Invertebrates, I have taken Scorpions of the genera *Hadogenes*, *Opisthocanthus*, *Parabathus*, and *Uroplectes*; Millipeds, Centipeds, Arachnids, and many insects.

After examination of the surrounding country had shown that Hounslow was far more densely inhabited than any other spot within a wide range, the question arose as to the reason for this, and there seemed to be three factors which accounted for it:—

1. The physical character of the rocks.
2. The abundance of small insect life.
3. The comparative rarity of snakes.

(1) The rocks have almost horizontal cracks, which have separated pieces ranging from 50 lbs. to several tons. The cracks may be several feet in length and depth, but are very narrow and hence afford ideal hiding-places for reptiles. In the wider ones are found *Pachydactylus hiberni* and *Zonurus cordylus* and in the narrower ones *Phyllodactylus essexi*. In these deep cracks these three species are safe from normal enemies. *Pachydactylus* and *Phyllodactylus* are nocturnal, and this in itself is some protection. *Zonurus* has a habit of sitting in the sun, but retreats head foremost into its crack as soon as it sees anything suspicious. In the crack it plants itself firmly by means of its claws, and if the tail be grasped in an attempt to pull the lizard out, the tail invariably breaks off. These diurnal lizards depend more on sight than on hearing for protection. I have stood, on several occasions, perfectly still within a few feet of *Pseudocordylus* and *Zonurus* and fired a pistol behind my back and the lizard has apparently taken no notice, but if the slightest movement be made the lizard vanishes. The reason for this is that the two most inveterate enemies of the lizards are birds, such as hawks and hornbills, and snakes, and in both cases the lizard is dependent on sight rather than hearing for protection.

(2) *Phyllodactylus essexi* is flattened dorsi-ventrally and gets into cracks, which are so narrow that only the smallest snake could get in to attack any lizard which had taken refuge there.

(3) The absence of snakes is accounted for by the absence of frogs, which is due to the absence of water. The only snake which from its rupicolous habit would be likely to become a menace to these reptiles is the Berg Adder (*Bitis atropos*). I have found this snake, which is probably the most primitive species of its genus, living in cracks on the tops of several mountains (e.g., on the Great Winterberg, 7800 feet), and its presence is always an indication of the paucity of lizards. For some reason this snake does not occur at Hounslow.

Scelotes cafer, *Glauconia nigricans*, *Typhlops delalandii*, and *Acontias meleagris* are all burrowing and insectivorous. Their burrowing habits make them safe, and the abundance of small insect-life makes it possible for them to find plenty of food. It might be argued that there should be a great deal of competition between the reptiles of similar habits. This does not seem to be so. Competition seems to be between closely-allied species rather than between genera of similar habits—for example, one never finds *Acontias meleagris* and *Acontias gracilicauda* together, although one does find *Acontias meleagris* and *Typhlops delalandii* in very close proximity.

Mabuia varia lives among the loose stones of a rough wall which crosses the area. I have watched *Mabuia varia* chase and eat spiders.

The prevalence of insect-life is due to the comparative wealth of vegetation whose dead organic matter provides food-material for many insects, and these in turn are eaten by other insects.

Hence one comes to the conclusion that these "Reptile Sanctuaries" require three conditions:—

- (1) Plenty of food-material.
- (2) Adequate hiding-places.
- (3) Comparative absence of enemies.

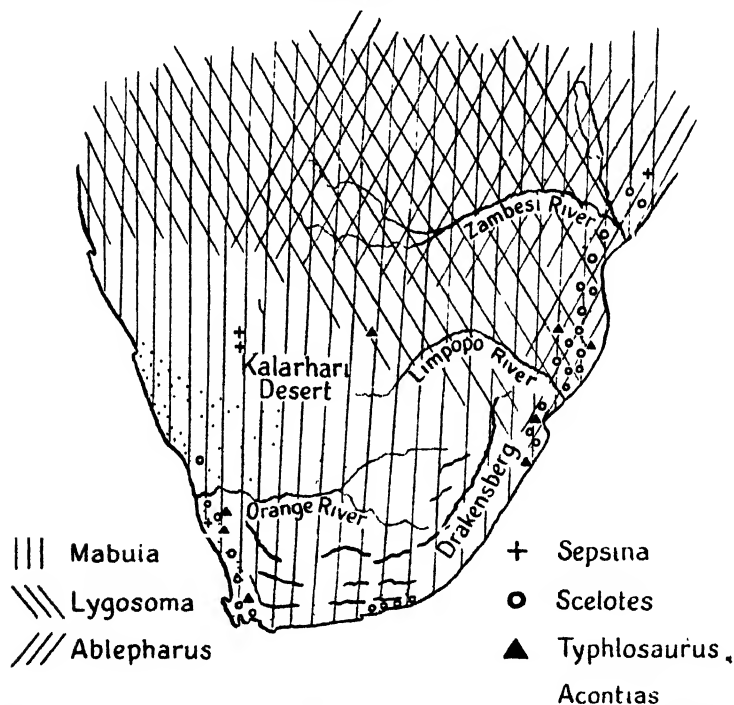
The second factor is, I think, the most important. It is not likely that in such spots as that mentioned above any evolutionary change takes place. Such spots would probably tend to fix and perpetuate a species rather than cause it to change.

The Geographical Distribution of Degenerate and Primitive Forms.

The distribution of Scincidae is shown on the map in fig. 85. There are seven genera in South Africa, of which four—*Sepsina*, *Scelotes*, *Typhlosaurus*, and *Acontias*—are more or less serpentine-form. It can be seen that the degenerate members of the family are nearly all situated round the coastal districts, while the normal limbed members are obviously dominant. This seems to point to the fact that the degenerate groups entered South Africa via

Mozambique and found it impossible to cross the watershed, and hence have remained on the coastal strip. When the migratory streams reach the Western Province they were deflected northward along the coast. But it will be noticed that *Acontias* is fairly prevalent north of the Orange River, and *Sepsina* and *Typhlosaurus* also occur in the Kalahari and Rhodesia. The explanation is, I think, that the streams of invasion split on the

Text-figure 85.



Distribution of genera of Scincidae in South Africa. The four genera, *Sepsina*, *Scelotes*, *Typhlosaurus*, and *Acontias*, are all more or less serpentiform and it is noteworthy that they are mainly coastal.

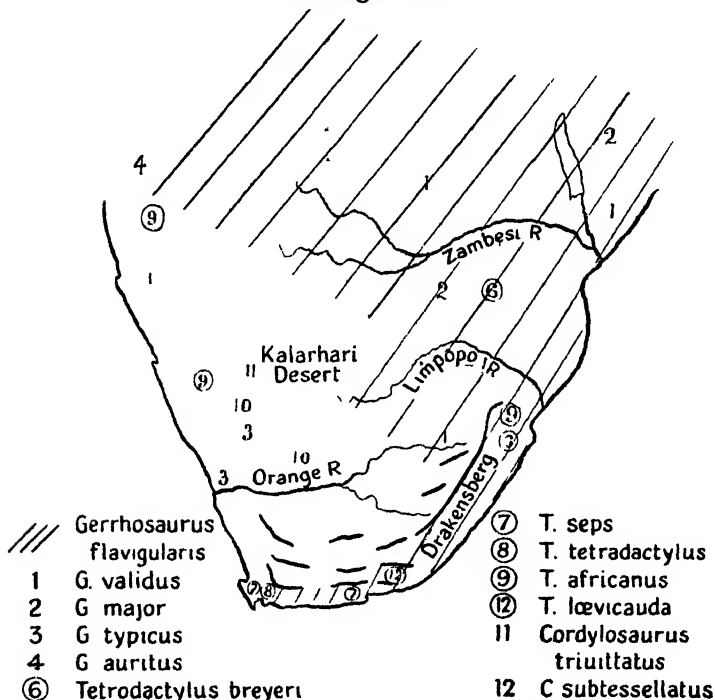
northern buttress of the Drakensberg and part went across Rhodesia, entered the Kalahari Desert, and suffered rather badly in crossing it.

Text-fig. 86 gives the distribution of the members of the Gerrhosauridae. The degenerate forms are represented by numbers in circles, and it can be seen that a similar state of affairs exists here as in Scincidae—i. e., the degenerate forms are again situated round the periphery of the sub-continent.

The Lacertidæ contains no degenerate forms, but of the Lacer-
tidæ *Tropidosaurus* is the most primitive member, and the author
found a new species of that genus on the summit of Mont-
aux-Sources, 11,500 feet, the highest point of Southern Africa.

An interesting case arises in the Zonuridæ, where the three
degenerate species of *Chamaesaura* are all situated on the south
of the watershed.

Text-figure 86.



Distribution of the Gerrhosauridæ in South Africa. The species marked by
numbers in circles are degenerate.

The degenerate genera mentioned above possess in most cases
several species, and hence it is imperative to examine the dis-
tribution-data of these species.

The Distribution of the Genus Acontias.

In order to read correctly the distribution data it is necessary
to determine which species of any given genus is the most
primitive and which the most recent. In the genus *Acontias*
this becomes fairly easy, in view of the fact that *Acontias* possesses
a degenerate pectoral girdle which varies in its degree of
degeneration in the various species.

After dissecting many specimens of *Acontias*, I am convinced that the degree of degeneration differs in each species and may be used, moreover, in determining the species. In considering these degenerate organs, it is obvious that the one which has the most reduced girdle must be considered to be the newest species, and the one with the best developed girdle must be the oldest and most primitive. The figures of the girdles of the South African species show that the order in which they must be placed, commencing with the most primitive, is:—

- (1) *Acontias breviceps* Essex.
- (2) *Acontias gracilicauda* Essex.
- (3) *Acontias plumbeus* Blanc.
- (4) *Acontias lineatus* Peters.
- (5) *Acontias meleagris* Linn.

It is significant that the most primitive is the mountain-top form, and that the most recent is the widest in its distribution, stretching from Damaraland to Mashonaland and from the Transvaal to the Transkei. Of the intermediate forms *Acontias gracilicauda* is known from the Eastern Province, and, although I suspect its distribution to be wider than at present known, I am certain that it does not extend as widely as *meleagris*. *Acontias lineatus* occurs in British Namaqualand and the western part of the Cape Province. There are various records of it from the Eastern Province, but I think it occurs very rarely, since I have taken at least two hundred and fifty *Acontias* in the Eastern Province, but have not yet taken *A. lineatus* there.

Schmidt ('Herpetology of the Belgian Congo,' 1923, p. 30) says: "It is impossible to escape the conclusion that these burrowing Scincidae have developed in South Africa and that their ancestors were present at a time of union of South Africa and Madagascar."

There are in Ceylon three species of *Acontias*, two of them possessing reduced limbs; in Madagascar there is one species.

I have some doubt as to whether Ceylon *Acontias* should be placed in the same genus as the South African ones, but, nevertheless, it is a closely-related Scinc and belongs to the same stock, and is progressing along the same evolutionary path. I think that it is more probable that the Ceylon species and the South African ones represent the ends of two divergent streams from an unknown centre, but whatever its origin I am inclined to believe that the *Acontias* came to South Africa from a north-easterly direction, and the first wave was *Acontias breviceps*, which, owing to the successive waves of *A. lineatus* and *A. meleagris*, found refuge on mountain-tops and is now almost extinct.

It is more than probable that some members of this genus of degenerated Scincs have become extinct, and one of the conclusions arrived at after a study of these degenerate forms is that the apparent discontinuity in Nature is due to the dying out of intermediate forms.

The Distribution of the Genus Scelotes.

The genus *Scelotes* includes the following species placed in order of degeneration :—

- (1) *Scelotes capensis* (pentadactyl).
- (2) *Scelotes tridactylus* (caffer) (tridactyl).
- (3) *Scelotes bipes* (two short hind legs).
- (4) *Scelotes brevipes* (two very short hind legs).
- (5) *Scelotes guentheri* (two bud-like rudiments).
- (6) *Scelotes anguina* (no external trace).
- (7) *Scelotes arenicola* (no external trace).
- (8) *Scelotes natalensis* (no external trace).

SCELOTES CAPENSIS is found in Gt. Namaqualand and on the west coast.

SCELOTES TRIDACTYLUS (CAFFER). Eastern Province and Bechuanaland.

SCELOTES BIPES. Western Province, Zululand.

SCELOTES BREVIPES. Mozambique.

SCELOTES GUENTHERI. Durban.

SCELOTES ANGUINA. South-eastern coast.

SCELOTES ARENICOLA. Mozambique.

SCELOTES NATALENSIS. Natal.

The genus *Scelotes* has given rise to several discussions with regard to the soundness of some of its species, and I am inclined to believe that the difficulty has been caused by the fact that some of the intermediates have not died out and hence some of the species are not clearly defined. However, the soundness of the species does not affect the consideration of the distribution-data. It is found that *S. capensis*, the most primitive member, is in the west, and that *S. tridactylus* is found in two widely-separated places—viz., the Eastern Province and Bechuanaland. The most degenerate are all found on the eastern coast, and, although they are not found in Phylogenetic order, it is noticed that the two most northerly species—*arenicola* and *natalensis*—are also the two most degenerate, and hence the most recent.

Again, one comes to the conclusion that the migratory wave came from the north-east and again split on the northern buttress of the Drakensberg, and although one cannot agree with Schmidt in regard to *Acontias*, yet there is reason to believe that the evolution of *S. arenicola*, *S. natalensis*, and *S. guentheri* may have taken place south of the equator.

The Distribution of the Genus Chamæsauro.

The genus *Chamæsauro* possesses four species—*C. tenuior* in Uganda, *C. ænea* in the Drakensberg Ranges, *C. anguina* in the southern coast-belt, and *C. macrolepis* in Zululand.

Of the South African species *C. ænea* is pentadactyl, *C. anguina* has one or two digits, while *C. macrolepis* has two hind limbs which when dissected show one or no digits.

Chamæsauro can be undoubtedly looked upon as the most primitive of the Zonuridæ. Camp (Class. of Lizards) argues that if one assumes *Chamæsauro* to be primitive one presupposes that the other members of the Zonuridæ have evolved from degenerate stock. The argument is not quite sound. *Chamæsauro* is a primitive Zonurid which became serpentiform to escape extinction, and the more normal Zonurids have evolved from similar primitive stocks which did not become serpentiform.

Of the South African species we again find the most primitive on the high mountains, and the next in order has already reached the Cape Peninsula and driven *C. ænea* to the mountains. The presence of *C. ænea* in Zululand cannot be explained as a third wave which will drive *C. anguina* to higher altitudes, but, I think, as a wave which started and became merely an isolated outpost. This *Chamæsauro* stream came along the same path as the others, but at an early stage it branched and *C. tenuior* became isolated in Uganda—and a certain amount of degeneration has obviously taken place in Africa south of the Equator.

CONCLUSIONS.

1. Degradation is a gradual process. Discontinuity is the result of the dying out of intermediate forms.
2. The main routes of migration into South Africa were:—one along the east coast and one across Rhodesia to the South-West Protectorate.
3. The most primitive members of any genus are found on the mountain-tops.

EXPLANATION OF THE PLATES.

PLATE I.

- Fig. 1. *Scelotes caffer*.
 2. *Scelotes bipes*.
 3. *Scelotes anguina*.
 4. *Scelotes brevipes*.

PLATE II.

- Fig. 1. *Chamæsauro anguina*.
 2. *Phyllodactylus essexi*.
 3. *Edura amatolica*.

PLATE III.

Sketch-map of routes of expeditions.

PLATE IV.

- Fig. 1. Looking down from the krantz at Mont-aux-Sources on to the Tugela River 2000 feet below.
2. A view of the Krantz.

PLATE V.

- Fig. 1. Looking up the Tugela Gorge at the krantz.
2. Another view of the Tugela Gorge.

PLATE VI.

- Fig. 1. Mont-aux-Sources, 12,000 feet.
2. The plateau on Mont-aux-Sources, 11,000 feet. The river in the middle distance is the Tugela.

PLATE VII.

- Fig. 1. The expedition at the summit.
2. The Reptile Sanctuary at Hounslow.

46. The Evolution of the Mammals in the Eocene.

By W. D. MATTHEW, F.R.S.*

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(Text-figures 1-16.)

The Tertiary Period is very appropriately known as the age of mammals. During that period the Mammals, previously a minor and unconsidered element in the land fauna, blossomed out into a great diversity of size, form, and habits, assumed the dominant position that had previously been held by the reptiles, and gave rise to the various existing kinds of higher quadrupeds as well as to numerous extinct races. The Eocene epoch, the early part of the Tertiary, witnessed the beginnings and early development of this great expansion, and is of particular interest to anyone trying to understand its nature and causes. A great deal of new evidence has come to light in recent years, through explorations in the Western United States and Canada, in Mongolia, Burma, and elsewhere, as well as through new discoveries in the older fields of Western Europe. Some of this evidence has been published or partly so; much of it has not. I have been so fortunate as to have had the opportunity to see and to study practically all of this new evidence, and in the following pages will attempt a brief outline of its salient points and the conclusions to which it seems to lead.

It is generally agreed that the origin of mammals was from the Theromorph reptiles of the later Palæozoic, and that among the Permian theromorphs of South Africa are to be found a number of small reptiles that may well have been the direct ancestors of the mammals. *Bauria*, *Ictidopsis*, etc., of the Upper Permian Karroo beds, have many mammalian features in teeth, skull, and skeleton, but have not yet the full status of mammals. The Upper Triassic *Dromatherium* and *Microconodon*, classic examples of the earliest of mammals, appear also to be rather pro-mammalian reptiles than true mammals†; but they are known only from the two lower jaws (three originally, but one disappeared) found by Emmons in 1857 in a coal mine near Raleigh, North Carolina. *Microlestes* from the Upper Trias of Germany is even less known, a few isolated teeth being quite insufficient to determine its characters of affinities. Perhaps it is truly a mammal, but no one really knows of what branch or evolutionary stage.

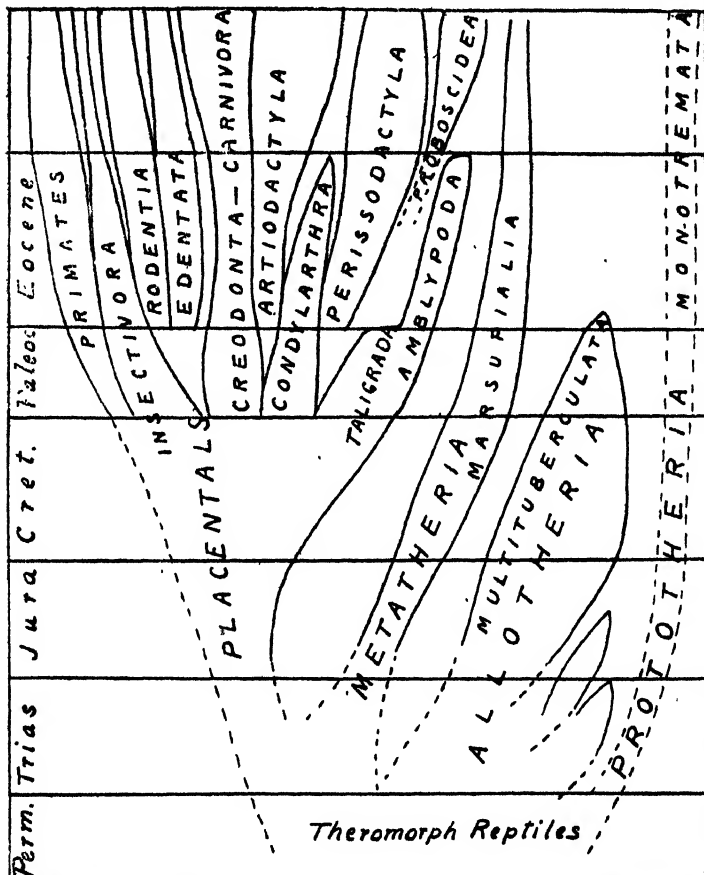
Our practical knowledge of mammals, then, begins with the

* Communicated by Prof. E. S. GOODE, F.R.S., F.Z.S.

† Simpson, 1926, Amer. Journ. Science, vol. xii. pp. 87-108.

Jurassic and Cretaceous, about the later half of the Age of Reptiles. The Jurassic mammals have been recently very thoroughly and critically revised by Mr. G. G. Simpson; I shall not attempt to summarize his conclusions, even to the extent to

Text-figure 1.

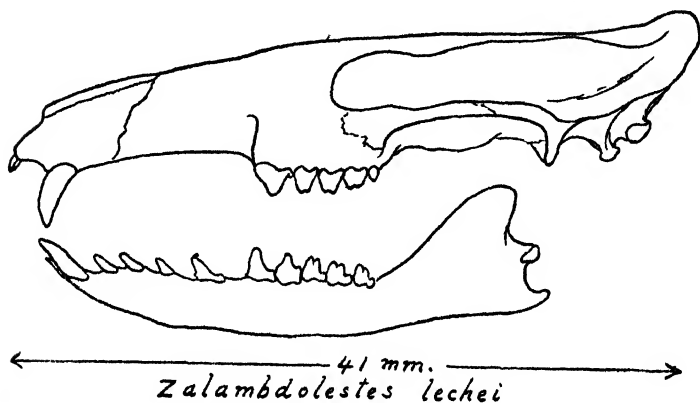


Progressive differentiation of the orders of Mammals during the Mesozoic and Tertiary. The orders were already distinct at the beginning of the Tertiary, although not so diversely specialized as they are to-day.

which I am acquainted with them, but will merely say that all the Jurassic mammals are of minute size and known chiefly from upper or lower jaws, representing a number of quite distinct groups or orders, among which may be the ancestors of the later mammals along with others clearly belonging to side branches.

Of these side branches the only one that needs any note here is the Multituberculata, an order of mammals that flourished in the Jurassic and Cretaceous, and survived into the beginning of the Eocene. Its affinities have been much disputed—regarded by some authorities as Marsupial, by others as ancestral to the Monotremata. Our present view is that the order represents separate stock or subclass of mammals, independently descended from the Theromorph reptiles, and co-ordinate with the Prototheria and Eutheria. The deciding evidence for this view rests chiefly in the structure of the pelvis, hind limb, and hind foot, known from fairly complete specimens in the Paleocene of Montana

Text-figure 2.



Skull and jaws of a primitive placental mammal from the Cretaceous of Mongolia. Note the long insectivore-like proportions and small brain-case. Reconstructed by Gregory and Simpson, 1925.

and New Mexico. The skull characters described by Gidley in *Ptilodus*, by Broom in *Taniolabis*, suggest affinities in some respects with marsupials, in others with monotremes, but can be consistently interpreted in conformity with the present hypothesis, which is the only explanation apparent of the curiously cynodont-like pelvis with its narrow-keeled pubo-ischial symphysis.

Cretaceous mammals have until recently been known only from isolated teeth and a few jaw fragments found in the uppermost Cretaceous*. The only positively identifiable specimens among these appeared to be marsupials and multituberculates, and this was also true of the few positively identifiable specimens from the Upper Cretaceous of the Red Deer River in Alberta. It was nevertheless quite possible that some of the small isolated teeth might belong to placental mammals.

* Lance formation. "Tertiary" of the U.S. Geological Survey official publications, but regarded by everyone else as Cretaceous.

The American Museum Expedition in Mongolia fortunately secured in 1924 a series of skulls of small mammals from one of the Cretaceous dinosaur deposits*. One of these is a multi-tuberculate; the others are small placental mammals that probably represent, in a general way at least, the ancestral type from which the early Tertiary mammals are descended. The multi-tuberculate calls for no especial comment; it is nearly related, so far as one can judge, to *Ptilodus* and its allies of the late Cretaceous and Paleocene faunas. The others are of a type somewhat intermediate between primitive Insectivora and primitive Carnivora. The skull has the long, almost tubular middle region of Insectivora, the reduced incisors, enlarged, sharp-pointed canines, cutting premolars of Carnivora, and the molars of a pretritubercular type approaching the zalambdodont Insectivora, but equally near to the early creodonts or primitive Carnivora. In one genus the last premolar is molariform, in two others it is simple; both conditions are matched among early Insectivora and creodonts. The molar pattern shows a high sharp pair of twin conical cusps, rather closely connate, the paracone and metacone of the tritubercular tooth, an angulate inner crescent, the protocone, and two strong ridges, the parastyle and metastyle, running outwards to the external angles of the tooth. The metastyle is lacking on M^3 . The fourth premolar is like the molars, save for less separation of the para-metacone and less extension of the protocone; in the anterior premolars the protocone disappears, the para-metacone is a single cusp, the styles reduced to small heels at the front and back of the tooth and then vanish, leaving only the single central cusp. This series, followed from front to back, gives obviously the evolution of the molars of these Cretaceous placentals, and the further change from these into the normal tritubercular teeth of Insectivora and of creodonts, and thence in diverse lines of specialization into the various types of molars of Tertiary and modern mammals is easily followed. It is not to be assumed, however, that all mammalian molars have followed through an exactly similar line of evolution. I shall instance one or two partial exceptions later, and there are others certainly or probably which have followed a somewhat different course. The zalambdodont Insectivora represent a partial reversion from the stage here shown. Their high central cusp is quite certainly the conjoined paracone and metacone, and not, as Cope and Osborn supposed, the protocone†.

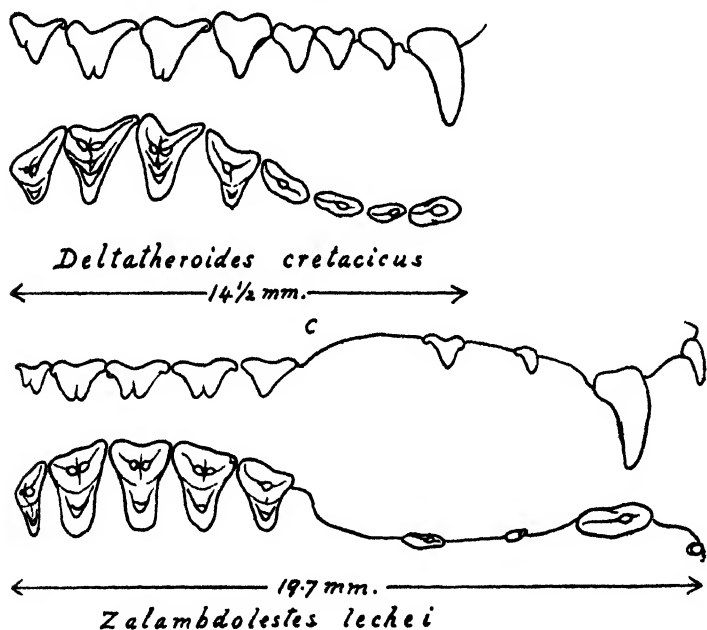
The lower teeth of these Cretaceous placentals are equally of a

* Simpson, 1925, A. M. Novitates, No. 201; Gregory and Simpson, 1926, A. M. Novitates, No. 225.

† This misunderstanding of the zalambdodont molar lies at the back of the one serious error in the otherwise admirable Tritubercular theory, causing the protocone to be regarded as the primary cusp of the tritubercular tooth. The central cusp of the zalambdodont tooth is the primary cusp, apparently and demonstrably, but it is not the protocone.

type from which those of Paleocene mammals can be derived. The molars have a high trigonid of two twinned cusps, protoconid and metaconid, a lower but prominent paraconid in front, a still lower crested and pointed heel of a single cusp, the hypoconid. In the premolars the high twinned protoconid and metaconid are represented by a single cusp, the paraconid by an anterior and the hypoconid by a posterior "heel," and the progressive simplification down to the single-cusped and single-rooted P_1 is well shown.

Text-figure 3.



Upper teeth of primitive placental mammals from the Cretaceous of Mongolia, showing the insectivore-creodont pattern from which the teeth of Tertiary mammals may be derived. After Gregory and Simpson.

These new Mongolian discoveries show then the ancestral type from which our earliest Tertiary mammals were derived. They are unfortunately not so well preserved that all the details of their skull structure can be ascertained. They have a small brain-case, the brain presumably of low type and without convolutions, the sagittal and occipital and lambdoid crests well developed, no postorbital processes to speak of, the orbit not being separate from the temporal region; the zygomatic arch is

complete but slender, the coronoid process broad and short—all conformant with a great development of the temporal and pterygoid muscles but relatively slight development of the masseter. This is the construction found among many modern insectivora.

Nothing is known as yet of the skeleton of these Cretaceous mammals, and but little of their habits. So far as the Mongolian fossils are concerned, the formation in which they occur is a wind-blown sand, and they are associated with nests and eggs of dinosaurs, with a number of different kinds of dinosaurs, carnivorous, armoured, and especially abundant ceratopsians, some lizards and small crocodilians, all the fauna such as one might find in a sand-dune area not very far from water. What the mammals were doing there is hard to say. Possibly they came from nearby swamps or forests to prey upon the small animals that would be attracted by the debris of a dinosaur nursery.

With this exception the Mesozoic mammals are found in association with a swamp fauna, and may be supposed from their occurrence and their general resemblance to modern arboreal and forest-living animals to have been tree-dwellers in the main, analogous to the modern opossums, tree-shrews, squirrels, etc., which in one way and another retain so much of the primitive mammalian character.

Such, then, were the ancestors from which our earliest Tertiary mammals were descended. We now turn to an examination of the first beginnings of mammals in the Tertiary, the so-called Basal Eocene or Paleocene faunas.

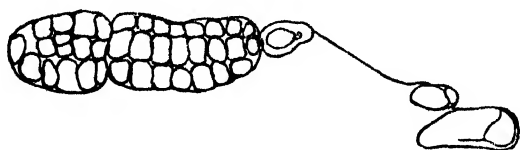
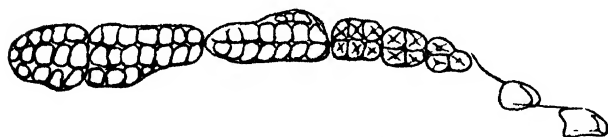
The importance of the Paleocene is hardly yet generally appreciated, and its title to rank as a distinct division or epoch of the Tertiary is not yet conceded by many, even of the vertebrate palæontologists, still less by the old-fashioned geologist. This is partly because the Paleocene faunas are still very imperfectly described or known to science, and partly because of an unfortunate early mistake as to the proper content of the term Paleocene. As originally defined it was made to cover not only the true Paleocene faunas and faunas then very slightly known, but also the lower part of the true Eocene. This was an unnatural association, and the division was artificial and unnecessary. In the more limited understanding here attached to it, and as used by a number of recent writers, it comprises the time between the end of the true Cretaceous and the beginning of the Suesonian, Wasatch, or Lower Eocene, properly speaking.

It is not necessary here to discuss the stratigraphic status of the Paleocene, or its connotation in the marine faunal succession between Cretaceous and Tertiary. We are here concerned only with its terrestrial vertebrates, and particularly the mammals. The Paleocene faunas cover the time between the final extinction of the dinosaurs and the first appearance of the principal orders of Tertiary and modern mammals. There are three horizons, as follows:—

	San Juan Basin, New Mex.-Col.	Wyoming.	Montana.	France.	Mongolia.
Upper Paleocene* ...	Tiffany.	Clark Fork.		Cernaysian.	
Middle Paleocene ...	Torreon.		Fort Union.		? Gashato.
Lower Paleocene	Puerco.				

The outstanding character of the Paleocene mammal faunas is this: They do not contain the ancestors of the principal orders of Tertiary and modern mammals, but diversified and rather specialized representations of more ancient orders which became extinct at the end of the Paleocene or lingered through the Eocene and then finally disappeared.

Text-figure 4

*Taeniolabis (Polymastodon) × 1**Ptilodus × 3*

Upper teeth of Multituberculate mammals of the Paleocene. Specialized survivors of a Mesozoic order.

In other words, the Paleocene mammals belong to Cretaceous orders. It is essentially the culmination of a Cretaceous mammal fauna, although living in the beginning of the Tertiary period as the lines are usually drawn.

The only modern orders are marsupials and Insectivora, which originated far back in the Mesozoic, and Carnivora, which are essentially Tertiary, but represented in the Paleocene by very primitive and archaic types. At the end of the Paleocene appear also a number of small Primates and primate-like Insectivora, more or less related to the modern tarsiers and tree-shrews, but

* The Tiffany fauna is found in the basal beds of the Wasatch formation. The Clark Fork fauna has in part the same relation; elsewhere it appears to be the upper part of the Fort Union formation. The Fort Union underlies the Wasatch in places, and overlies the latest dinosaur beds (Lance). The Torreon underlies the Wasatch, and the Puerco underlies the Torreon and overlies very late dinosaur beds (Ojo Alamo). Stratigraphic and faunal breaks are not always conformant. There is no real reason why they should be, although many geologists seem to think it necessary.

known only from upper and lower jaws, so that their evolutionary stage and affinities are not really known with certainty in spite of very positive statements made about them. They may yet prove to be sub-primates or pseudo-primates.

II. Conspectus of Paleocene Mammals.

1. LAST MULTITUBERCULATES. $\left\{ \begin{array}{l} \textit{Tæniolabis} \text{ etc.} \\ \textit{Ptilodus} \text{ etc.} \end{array} \right. \left\{ \begin{array}{l} \text{Larger; premolars} \\ \text{reduced.} \\ \text{Smaller; cutting} \\ \text{premolars.} \end{array} \right.$

Pseudo-rodents with gnawing front teeth, grinding molars, premolars vestigial in *Tæniolabis*, but a large cutting lower premolar in *Ptilodus*. Broad, triangular skull. Narrow, deep pelvis like theromorph reptiles. Five toes; astragalus is small, flat, like some marsupials. Remnant of a fifth distal tarsal, external to the cuboid, ?.

2. MARSUPIALS are small, scarce, related to opossum, but teeth are more typically tritubercular in that the paracone and metacone are of equal size. They are a remnant probably of Cretaceous marsupials, but too imperfectly known to show whether they are closely related or not.

3. CREODONTS OR PRIMITIVE CARNIVORA.

A. Oxyclænids—*Deltatherium*, *Chriacus*, *Oxyclænus*.

The teeth are primitive tritubercular, not unlike those of lemurs. The skeleton is of primitive carnivore type—slender limbs, long tail, long slim body, plantigrade five-toed feet with long phalanges and sharp claws. Brain smaller than in later carnivora.

B. Arctocyonids—*Clænodon*, *Protogonodon*.

Flattened crowns on teeth, somewhat bear-like. Skull and skeleton on same lines as Oxyclænids, but more massive.

C. Miacids—*Didymictis*.

This family is ancestral to true carnivora; true carnassial

teeth $\frac{P^4}{M_1}$, and first appears in the Middle Paleocene with the single genus *Didymictis*.

D. Mesonychids—*Dissacus*.

No shearing-teeth, round high-pointed cusps, peculiar feet with more compact metapodials, a curiously artiodactyl-like construction of the tarsus; the gait was apparently digitigrade.

4. CONDYLARTHES. *Tetraclænodon*. Four-cusped symmetry of molars.

Crushing pig-like teeth, with six round cusps on upper molars, four on lower. Skeleton very like that of the

Text-figure 5.



Hemithlæus $\times \frac{2}{1}$



Ectoconus $\times \frac{1}{1}$



Tricentes $\times \frac{2}{1}$



Tetraclænodon $\times \frac{1}{1}$

Upper teeth of Paleocene trituberculatos. *Hemithlæus* and *Ectoconus* are Lower Paleocene Taligrada. family Periptychidæ; *Tricentes* a Middle Paleocene creodont, family Oxyclenidæ; *Tetraclænodon* a Middle Paleocene condylarth family Phenacodontidæ.

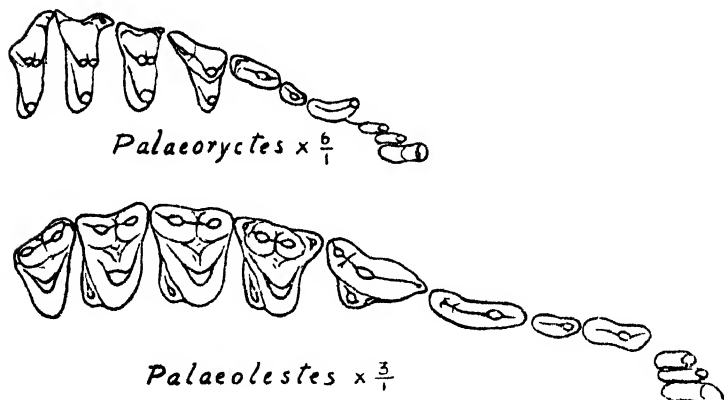
creodonts, claws somewhat broadened, and feet compacted, digitigrade, the side toes reduced. This animal is the direct ancestor of *Phenacodus* of the true Eocene.

5. TALIGRADES. *Ectoconus*, *Periptychus*.
Haploconus, *Anisonchus*, etc.
Pantolambda, *Miocænus*.
Ellipsodon.

Molars mostly of crushing type with round cusps; in *Pantolambda* sharply crescentic. Always a triangular symmetry on upper molars. Premolars enlarged in *Periptychus* and smaller relatives and in *Miocænus*, but not in other nearly related genera.

All five-toed, plantigrade, digits shortened in the larger genera and very short in *Pantolambda*, which is related to the Amblypods. Hoofs, not claws, on the toes in the larger genera, unknown in the others.

Text-figure 6.



Upper teeth of Paleocene Insectivora. Early representatives of the zalambdodont and erinaceoid groups.

These are the most abundant animals in the Paleocene, but have no descendants in the Eocene.

6. AMBLYPODA. *Prodinoceras* in Wyoming and Mongolia.
 Ancestor of uinatheres of Middle and Upper Eocene. The pattern of the upper teeth in these dinocerata is very curious. It appears to be wholly lacking in protocone, according to one possible interpretation; but it can also be interpreted as with tritubercular molars.
7. INSECTIVORES.
Palaeolestes. Tritubercular teeth, molariform P_4^4 , related to Leptictidae and ? hedgehogs.

Palaeoryctes. Zalambdodont teeth, skeleton unknown.

Two or three other genera related to *Palaeolestes*, but little known, including *Myrmecoboides*, which is not a marsupial but a leptictid insectivore. Skeleton of *Palaeolestes* is primitive insectivore, shown by tibia and astragalus and short toes. Here also belong

Onychodectes and *Conoryctes*, transitional in some ways to *Tæniodonta*.

8. TÆNIODONTA. *Wortmania* and *Psittacotherium*.

Aberrant group paralleling ground-sloths.

Whether the *Tæniodonta* can be considered a suborder of *Edentata* is open to question, but, if so, their relationship is more distant than that of the *Pholidota*. More probably they have none beyond a common descent from Cretaceous pre-Insectivora.

9. MENOTYPHLA.

Plesiadapidæ are semi-Primates with enlarged, somewhat rodent-like incisors.

Nothodectes = *Plesiadapis*.

This genus is known from several incomplete skulls and parts of the skeleton in the Upper Paleocene of Colorado. There are several other genera known from jaws or parts of jaws only which appear to be nearly related. The skull and skeleton characters of "*Nothodectes*" come nearest on the whole to tree-shrews, but approach the lemurs and tarsioids to some extent. A fairly strong argument could be put up for inclusion of this genus and all the plesiadapid group in the order Primates, although not, I think, for associating them with *Chiromys*, as is done by so high an authority as Stehlin. *Chiromys* appears to be a true lemur, aberrant only in the rodent-like incisors, a parallel specialization to the *Plesiadapidæ*, but in all probability of much later origin.

10. TARSIOID PRIMATES.

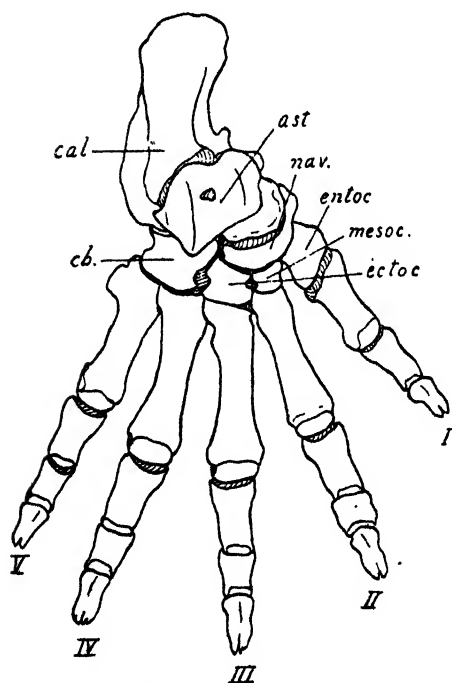
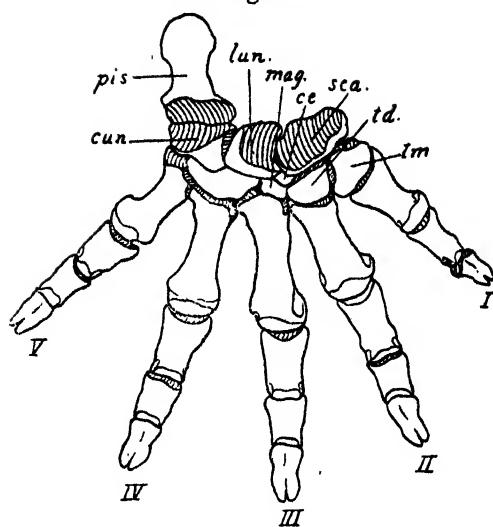
Appear in Upper Paleocene, several minute genera, known only from upper and lower jaw fragments. Primate-like in teeth, but it is yet to be proved that they are really in a primate stage of evolution in skull and skeleton or in brain-characters.

11. CHIROPTERA.

Zanycteris, front of skull. Related to *Phyllostomine* bats. Some doubtful wing-bones associated.

These Paleocene faunas are of great interest as being the oldest large and adequately known mammalian faunas. They

Text-figure 7.



Fore and hind feet of *Ectocoenus*, a primitive ungulate (order Taligrada) from the Lower Paleocene. One-half natural size.

are nearly all very primitive, with low-crowned teeth, tritubercular molars, generally unreduced dentition, five-toed plantigrade feet, small brain-case, and many primitive characters in skull and skeleton. When first discovered by Cope, it was anticipated that they were the ancestors of the Lower Eocene mammals; Osborn pointed out later that this was true only in small part, and regarded them as representing a "Mesoplacental" adaptive radiation, in contrast to the "Cenoplacental" radiation which resulted in the higher mammalian orders. Like most generalizations this was inexact, but it has been substantially confirmed by later studies. These Paleocene mammals belong mostly to extinct orders. The multituberculates and the numerous kinds of Taligrada disappear at the beginning of the Eocene. The oxyclonid and arctocynid creodonts and the phenacodont condylarths last through the Lower Eocene, the mesonychid creodonts, the Dinocerata, and the Taniodonts until the end of the Eocene, while insectivores, marsupials, bats, primates, and the miacid pro-Carnivora survive to the present day. But the bats and primates appear first in the Upper Paleocene, the miacids only with a single species in the Middle Paleocene, and there is nothing, as we shall see, to represent the ancestry of the greater part of the Eocene and later Tertiary mammals.

The three successive faunas of the American Paleocene—superposed stratigraphically, so that there is no question as to their sequence—enable us to trace the progressive evolution and specialization of many phyla, the appearance of some, the disappearance of others, the modification from one stage to the next of those that pass through. Examining many hundreds of specimens for identification and cataloguing, one is impressed with the fact that in old and unprogressive phyla approaching extinction the species characters are much more definite and fixed, the species vary but little and are easily distinguished, in contrast with new, progressive, and rapidly expanding groups, in which individual variation is rampant and species very difficult to distinguish.

In Europe the only Paleocene fauna is the Cernaysian of northern France, which appears to correspond with the Upper Paleocene of America, and in large part consists of identical or nearly related genera. Like the American Paleocene, it fails to show the ancestors of the greater part of the Tertiary mammalia.

It had been expected that the ancestry of the Eocene mammals would be found in Central Asia, but the newly-discovered Paleocene fauna of Mongolia is of curious and unexpected type. It contains a small multituberculate *Prionessus*, related to the Upper Cretaceous *Meniscoessus*; a little animal, *Eurymylus*, possibly related to the tree-shrews; a supposed Taligrade, *Phenacolophus*, and a very small supposed Creodont, *Hyracolestes*; a large zalambdodont Insectivore (un-named); and one or two other doubtful forms, none at all nearly related to the European

or North American Paleocene animals, and still less to the Eocene or later faunas. But the most abundant animal is a tiny notoungulate, *Palaeostylops*, related to certain of the peculiar ungulate animals of Tertiary South America. The discovery of this animal, ancestral to a part of the South American Eocene mammals, in a fauna that does not contain the ancestors of the North American Eocene mammals, would be more puzzling were it not for our finding some years ago in the Lower Eocene of Wyoming a single lower jaw (*Arctostylops steini*) which is evidently a direct descendant of the Mongolian *Palaeostylops*, and is in turn more primitive and at least in a broad way ancestral to *Leontinia* and its allies of the South American Eocene (probably Upper Eocene, although regarded by Ameghino as Cretaceous). This suggests that these South American Eocene ungulates really came from North America, although for the most part their ancestors have not been found; and that in turn the North American and European mammals came in large part from Asia, although we have not found them in the known fauna.

III. The Eocene Mammals.

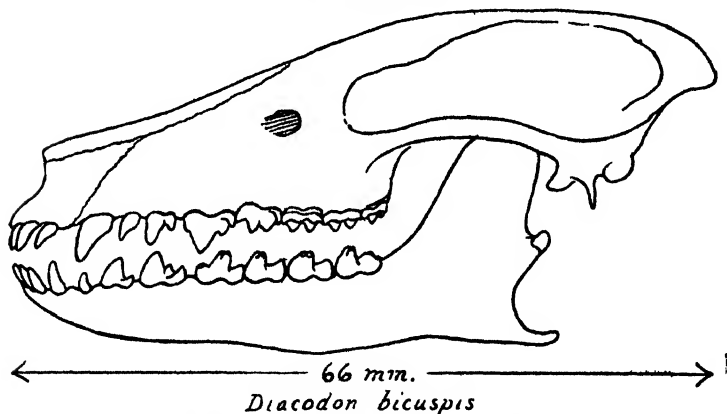
With the beginning of the true Eocene comes in a great new mammal fauna. It appears quite suddenly, apparently due to a great invasion which brings in for the first time the direct or nearly direct ancestors of the principal groups of Eocene and later Tertiary mammals—that is to say, the Perissodactyla, Artiodactyla, rodents, edentates, and unmistakable primates. As we have seen, some forerunners of the Carnivora and Primates and the earliest recorded Chiroptera had already appeared in the later Paleocene, but now the more progressive creodonts and the typical lemuroid Primates appear in force. The Lower Eocene fauna is best known from the Wasatch and Wind River formations in Wyoming and New Mexico, but the European Lower Eocene of the London Clay, the Paris Basin, and southern Belgium, so far as it is known, is identical—that is, all the European genera are found in North America. This is only explainable as the result of a great migration from some common source, intermediate geographically. Atlantis if one prefers an imaginary continent, Asia if one prefers a really existing one, may be regarded as this centre of dispersal. South America, Africa, and Australasia are out of the question, for the new faunas did not reach any of those continents until later—have hardly yet reached Australia.

Wherever they come from—a point we shall return to later—these new groups of mammals were already well distinguished as orders. The perissodactyls had already the typical perissodactyl astragalus fully developed, and their teeth already show the fundamental pattern of the perissodactyl molar. They have four digits in the front foot, no remnant left of the pollex, and

in the hind foot only three complete digits, but small splints representing the missing first and fifth.

The artiodactyls similarly show a fully-developed artiodactyl astragalus, and considerable reduction of the side toes on an artiodactyl symmetry; but their teeth are very primitive—still tritubercular in type. The rodents again have the astragalus typical of the order and the even more characteristic gnawing incisors fully developed, with as much reduction of the other front teeth as in the more primitive of the modern rodents. And the lemuroid Primates likewise display the ordinal characters—the large opposable thumb and great toe provided with nail instead of claw, the reduction of the incisors to $\frac{2}{2}$, the long, slender, straight limb-bones and various other skull and

Text-figure 8.



Skull of *Diacodon*, an erinaceoid insectivore (family Leptictidæ) from the Lower Eocene. Descendant of *Palæolestes* of the Paleocene.

skeleton characters. The ordinal characters of the new groups are well developed. But beyond this they have not gone; the families are not yet differentiated.

IV. Conspectus of Lower Eocene Mammals.

1. MULTITUBERCULATES.

One specimen, *Eucosmodon* sp., survives into the beginning of the Wasatch.

2. MARSUPIALS.

A few jaw-fragments of small species related to the opossum have been found.

3. CREODONTS.

A. Hyænodonts. *Sinopa* abundant.

Unreduced tuberculo-sectorial dentition, carnassial teeth M_2^2 .

B. Oxyænids. *Prolimnocyon*, *Dipsalidictis*.

Tuberculo-sectorial dentition, carnassial teeth M_2^1 , molars behind them reduced or absent; molar formula M_3^{2-3} .

Oxyæna.

Larger, more sectorial teeth, M^2 transverse, M - absent.

Palæonictis, *Amblyctonus*.

Shorter face, high piercing cusps, M^2 vestigial, M_3^3 absent.

C. Arctocynidæ. *Anacodon*.

Last survivor of the family. Flattened tubercular teeth, sabre-like upper canines.

D. Mesonychidæ. *Pachyæna* and *Dissacus*.

Larger, more specialized survivors of the Paleocene Mesonychidæ.

E. Miacidæ. Carnassials P^4 , M_1^7 , as in modern Carnivora.

Didymictis and *Viverravus*; viverroid teeth; M_2^2 .

Miacis, *Vulpavus*, *Vassacyon*, *Uintacyon*. Ancestral to true Carnivora. M_3^3 . Skeleton in *Didymictis* more running type, brain smaller. In *Miacis* group the skeleton is more of a climbing type, the brain well developed for an Eocene carnivore.

4. CONDYLARTHS.

A. *Phenacodus* is a descendant of *Tetraclænodon*.

Five toes, but lateral digits are reduced. Teeth develop accessory cusps, polybuny. Brain very small, no convolutions. Ungual phalanges are small flattened hoofs, the toes short, foot compact, head relatively small, tail long. Mostly of larger size omnivorous terrestrial animals adapted for walking and running.

B. *Hyopsodus* has gone in the opposite direction, a small animal about the size of a hedgehog, with simple six-cusped teeth. Has been considered a Primate, and also an Insectivore, but real affinities seem to be with the Condylarths,

though it is clawed, not hoofed. This is the most abundant animal in the Eocene, and is regarded as semi-arboreal, like the tree-shrews.

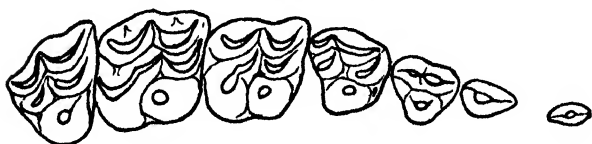
O. Meniscotherium: short head, crescentic cusps of peculiar pattern; possible relations with the Notoungulata. Needs critical re-study and comparison with Hyracoidea.

5. AMBLYPODA.

These take the place of the Taligrada, though much more specialized, and not direct descendants.

A. Bathypsis. Descended from Paleocene *Prodinoceras*. The molars are small, of a peculiar pattern; large dagger-like upper canines; the skull shows small bosses prophetic of the horns of *Uintatherium*.

Text-figure 9.



Meniscotherium $\times \frac{3}{2}$



Phenacodus $\times \frac{1}{1}$

Upper teeth of Lower Eocene condylarths. *Phenacodus* is a descendant of *Tetracænodon* of the Paleocene.

B. Coryphodon. Larger teeth, front teeth of Hippopotamus-like pattern, elephantine feet and legs. The largest animal of the Lower Eocene. *Coryphodon* is related to *Pantolambda* of the Paleocene, but not a direct descendant.

6. PERISSODACTYLS.

These appear suddenly and in great abundance at the beginning of the true Eocene. Ordinal characters are already well defined, but family characters are not yet differentiated.

Eohippus. Commonly known as the four-toed Horse, but it might also stand as ancestral to tapirs, rhinoceroses, titanotheres, etc. *Homogalax* is said to be ancestral to tapirs, but it is doubtful whether it is any more related to them than is *Eohippus*. *Heptodon*, which appears a little later, is a little nearer to the rhinoceroses. But probably none of these genera is directly ancestral to the later Tertiary Perissodactyls, and all of them are more or less approximately so. *Eohippus* has toes four-three, with traces of digits one and five on hind foot, but no trace of the missing toe (pollex) on the fore foot. *Homogalax* and *Heptodon* are practically indistinguishable from *Eohippus* in the feet. Front teeth are alike in all of them, and so with other parts of the skeleton that are known. Fibula is complete and separate from tibia, and radius and ulna are entirely separate.

7. ARTIODACTYLS.

Diacodexis is a tiny animal, about the size of a rabbit, with primitive bunodont, tritubercular teeth. So primitive that it has been referred, at different times and under different names—*Pantolestes*, *Trigonolestes*, etc.—to Primates, Creodonts, Insectivora, and was positively recognized as Artiodactyl only by the characteristic hind-foot bones associated with the teeth. The astragalus is quite unmistakably artiodactyl. The toes are probably four-four, but the side toes in the hind foot are reduced to slender vestiges; in the fore foot they are still good-sized. This would exclude *Diacodexis* from being ancestral to all Artiodactyls, as several families of this order have four well-developed toes on each foot, and even a complete pollex is present in some of the genera (*Oreodon*, *Ancodus*, etc.). There are, however, other larger genera of Artiodactyls in the Lower Eocene which appear to be nearly related to *Diacodexis*, but only the jaws are known, and some of these might have the toes unreduced. It seems, therefore, that the Artiodactyls in the Lower Eocene, like the Perissodactyls, had not yet separated out into families, though the order was well differentiated.

8. RODENTS.

Represented in the Lower Eocene by *Paramys*, which has short-crowned teeth of squirrel-like pattern and a skull much like that of a squirrel or marmot, but with the antorbital region like that of the dormice. This I regard as the primitive type from which all our simplicitentate rodents may be derived*. The limbs and feet are squirrel-like, the toes four in front and five behind. The rodents

* Miller and Gidley do not accept this interpretation, but Schaub's recent work on the Cricetidae appears to support it.

appear to be derivatives of insectivore stock well back in the Cretaceous.

9. EDENTATES.

Apparently the beginnings of the Edentate stock in the genus *Palaeonodon*. Cheek-teeth reduced to a row of small peg-like enamel-less teeth, probably but not certainly a larger canine in front with enamel on the front. Skull and skeleton have the peculiar characters of armadillos and pangolins in a much less advanced stage—only one step removed from Insectivora, so that it might be a question whether they really are Edentates or only edentate-like Insectivores. However, they are certainly ancestral to *Metacheiromys* of the Middle Eocene, which is so definitely armadilloid in skull and skeleton that I think it is hardly open to reasonable doubt, although it cannot be directly ancestral, at least to the armadillos. If *Palaeonodon* is a true Edentate, it points to the derivation of the order from primitive Insectivores of the late Cretaceous.

10. TENIODONTA continue on from the Paleocene, a curious specialized group of disputed relationship. They parallel the ground-sloths in adaptation, but probably are not Edentates. Thornton Carter's evidence on enamel structure indicates that they are not near to any other placentals.

11. INSECTIVORA.

Not very much known because of the fragmentary material, but there seems to be a considerable variety of them. The Leptictidæ continue on from the Paleocene, and there are several other types of very uncertain relationship, placed here for lack of a better place.

12. MENOTYPHLA.

The modern Tupaiidæ. A considerable number of small mammals in the Lower Eocene seem to be intermediate between *Tupaia* and *Tarsius*. Not enough is known of their skulls or skeletons to be sure whether they are Menotyphla or true Primates. Family Plesiadapidæ.

13. PRIMATES.

True lemuroid Primates are certainly represented by *Pelycodus*. Like its successor *Notharctus* of the Middle Eocene, it has only two incisors, and many lemur characters in the teeth and skull, and the skeleton quite of Primate type, with the opposable hallux and pollex, nail-bearing and of larger size than the other digits, primate astragalus, and long slender limbs. This group of true Primates appears suddenly in the Eocene and has no known Paleocene predecessors. The tarsiid Primates are certainly

represented by *Tetoni* and probably by *Omomys* and other genera, and, as we have seen, these Tarsiids seem to have made an earlier appearance in the Paleocene and to be connected with the Plesiadapidae, which bridge the gap between tree-shrews and Primates.

14. TILLODONTS are another group of uncertain relations, probably not far from Insectivora, appearing first in the Lower Eocene as *Esthonyx*. They parallel the rodents in some ways, enlarging front teeth into gnawing incisors, but are not related to them.

These Eocene mammals are partly descended from the Paleocene fauna—some of the Condylarths, some of the Creodonts, some of the Amblypods, some of the Insectivores, etc. These are mostly larger and more specialized than their Paleocene ancestors. But the greater part are new invaders that must have evolved in some other, unknown, region and appear first in North America and Europe at the base of the Wasatch or Sparnacian stage. These invading groups are the Perissodactyls, Artiodactyls, Rodents, lemuroid Primates, Tillodonts, and Edentates. That is to say, they are the orders that play the principal part in the Tertiary history of mammals, and include nearly all the existing mammals except Carnivora and Chiroptera. It is fair to say that the principal orders of modern mammals appeared first at the beginning of the true Eocene, and that this is the point where the Age of Mammals really begins. The Paleocene fauna is mostly composed of survivals from a Cretaceous mammal evolution, some of which linger through the Eocene, but it does not contain the ancestry of the modern mammals.

The first evolution of these Tertiary orders of mammals must have taken place in some region unknown to us, perhaps Asia or various parts of the northern Holarctic. They appear in the Lower Eocene, with the *ordinal* characters already distinct. But the *family* characters have not yet evolved, and these family characters were differentiated during the Tertiary. Among Perissodactyls they were differentiated during the Eocene. Some of the Artiodactyl families can be traced back into the Eocene, most of them arose later, and the same holds true of the Rodents, Carnivora, and Primates.

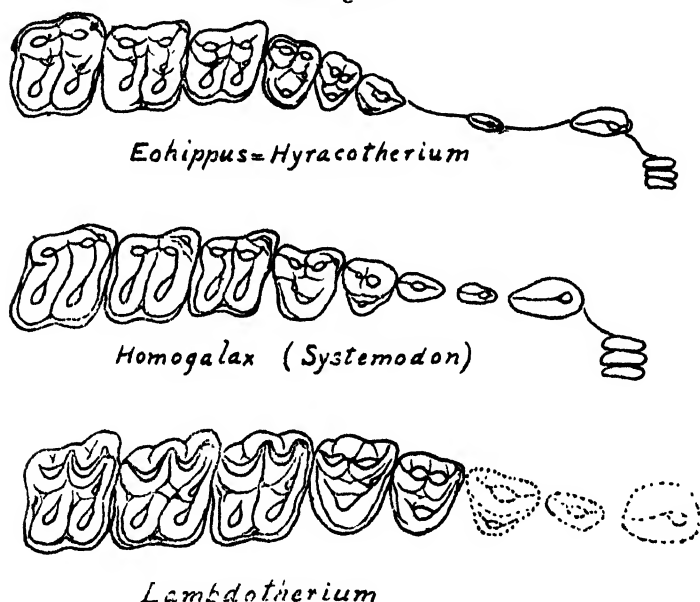
V. Evolution of Mammals through the Eocene.

We are able to trace the successive evolutionary stages of many "phyla" (lineages) in North America and Europe. Starting from a common source in the Lower Eocene fauna, they become progressively divergent and specialized into several families by the end of the Eocene. The faunas of Western Europe and of North America, almost identical at the beginning

of the Eocene, have become quite distinct by its close, evolving on more or less parallel lines, but into distinct groups.

Some of these phyletic series are well known. The evolution of the Four-toed Horses, or Hyracotheriines, has been traced in America through successive stages in the Lower, Middle, and Upper Eocene—*Eohippus*, *Orohippus*, *Aminippus*, and *Ephippus*,—the progressive molarization of the premolars and some reduction of the lateral digits being well shown. On one side of this Hyracotheriine series a somewhat less satisfactory series leads up through *Heptodon*, *Hyrachyus*, *Amyrnodon*, *Cænolophus*, and other genera into the rhinoceroses, and, on the

Text-figure 10.



Lower Eocene Perissodactyls—*Eohippus* ancestral to the Equidae, *Homogalax* related to the Tapiridae, and *Lambdotherium* ancestral to Titanotheriidae.

other side, a series through *Lambdotherium*, *Eotitanops*, *Palaesyops*, *Telmatherium*, *Diplacodon*, and others into *Titanotherium* of the Oligocene. Intermediate lineages leading into the tapirs, the colodons, and some lines that did not survive the end of the Eocene have not yet been cleared up; and in Europe, Stehlin has shown a number of distinct phyla of palæotheres and lophiodonts. Much remains to be done before the phylogeny of Eocene Perissodactyls can be traced in detail, but its broader lines show a progressive divergence from a common ancestral type represented

by *Hyracotherium* or *Eohippus* into the distinct families of titanotheres and chalicotheres, horses and palæotheres, tapirs and lophiodonts, hyracodonts, amynodonts and true rhinoceroses that are found at the end of the Eocene or beginning of the Oligocene.

There is less evidence bearing on the evolution of the Artiodactyls through the Eocene than is the case with the Perissodactyls, and it is less easy to distinguish and trace the divergent phyla. In a broad way it follows somewhat the same lines, leading up into the two divergent groups, the suillines and the ruminants, and with a confusing complex of intermediate phyla which mostly die out about the end of the Eocene, some surviving later into the Tertiary. From the early selenodonts of the late Eocene branch came progressively the camels, tragulids, deer, giraffes, and antelopes, sheep, and cattle, the last three constituting the great bulk of modern ruminants. The suillines split into pigs and peccaries, and from somewhere between the two the hippopotami derive. But most of these modern groups are not yet differentiated at the end of the Eocene, and the intermediate groups play an important part in the fauna. Among these may be noted the anthracotheres of pig-like proportions in skull, limbs, and feet, but with a sub-crescentic pattern on the teeth that links them with the ruminants. These and the allied anoplotheres, xiphodonts, etc., are common in the Old World Eocene. Anthracotheres survive, especially in the Orient, until the later Tertiary, and reach America in the Oligocene. Curiously enough they are not found in Mongolia*, although they are common in Europe, Egypt, India, and Burma, as well as in North America. The entelodonts, or giant pigs, are another interesting group of artiodactyls, although chiefly found in the Oligocene and Lower Miocene. They had a relatively huge skull, with teeth almost like those of an omnivorous carnivore, and in proportions of the body and limbs and the two-toed feet are more suggestive of a bison than anything else. Another of the intermediate groups that has its origin in the Eocene is the oreodonts or ruminating hogs of America, with ruminant cheek-teeth, but a short, peccary-like skull and tusks, and compact body, short legs, and four-toed feet like the pigs. On the whole it would seem that this order had made less progress than the Perissodactyls by the end of the Eocene, and wasted most of its energies, if one may say so, in unsuccessful experiments.

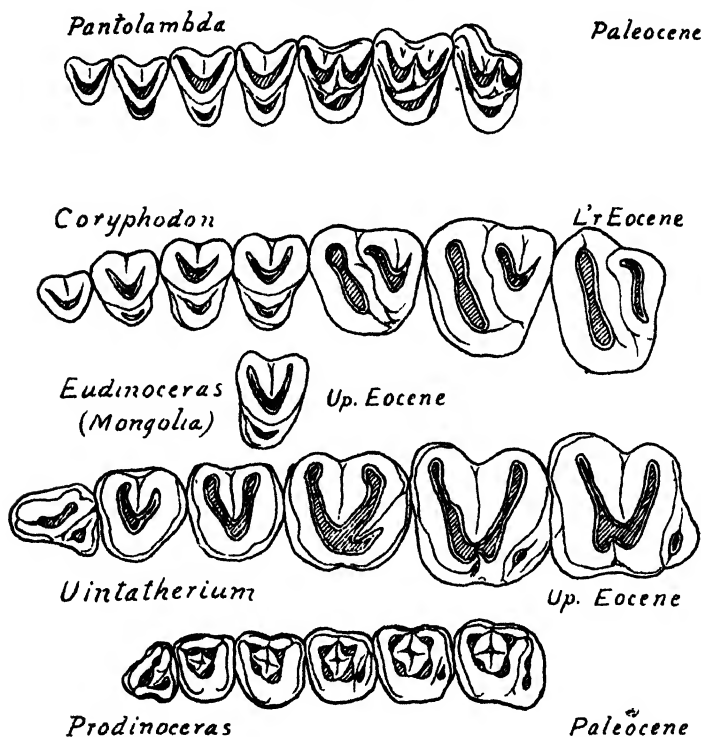
The Condylarthra, surviving through from the Paleocene, play an important part among the Lower Eocene mammals, but then disappear from the stage, except for the little *Hyopodius* with its rather lemur-like teeth and skull, with skeleton more like Insectivora and habits perhaps arboreal.

The Amblypoda are the largest animals of the Eocene. *Coryphodon* of the Lower Eocene is as large as modern cattle, with a

* Save for one doubtful molar tooth.

flaring, hippopotamus-like muzzle and tusks, and proportioned somewhat like a Kadiak bear, except for the shorter legs and the rounded, compact, five-toed, elephant-like feet. This animal is found in the Lower Eocene of America and Europe, coming in with the true Eocene fauna, and without any known ancestry in the Paleocene, although *Pantolambda* and *Titanoides* are rather

Text-figure 11.



Upper teeth of Amblypoda. The Eocene *Coryphodon* is probably related to *Pantolambda* of the Paleocene, and the Eocene *Uintatherium* appears to be a descendant of *Prodinoceras* of the Paleocene (Wyoming and Mongolia). Premolars and molars in coryphodonts and uintatheres evolved on independent lines as shown by comparison of these figures, which confirm the views of H. E. Wood as to the interpretation of the *Uintatherium* molar.

definitely related. Nor are there any known descendants in the later Eocene of Europe and America. Recently, however, a probable descendant has been discovered in the *Eudinoceras* of the Upper Eocene of Mongolia, which turns out not to be related to the Dinocerata, but a coryphodont, not very different from the Lower Eocene genus. The evolution of the molars in this group

is not very clear. Apparently they are derived from something of the *Pantolambda* type, by uniting the anterior limbs of the paracone and protocone crescents into a single crest, and loss of their posterior limbs, the metacone crescent remaining little changed or losing its anterior limb.

In the other phylum of Amblypoda the molars have apparently a quite distinct history. Beginning with the rather small Paleocene *Prodinoceras* of Mongolia and Wyoming, they appear again in *Bathyopsis* of the Lower Eocene, *Uintatherium* of the Middle Eocene, an *Eobasileus* of the Upper Eocene, progressively increasing in size and massiveness, and developing great horn-bosses on the skull, three pairs in the latest stage, which is as large as a rhinoceros, and of somewhat the same proportions save for the more compact five-toed feet very like those of *Coryphodon*, but with the toes still further reduced. The teeth do not change very greatly in this series. The upper canines are long, compressed, dagger-like tusks, protected by a flange in the lower jaw. The cheek teeth all have the same peculiar pattern, essentially a single high, crescentic inner cusp extended externally in long ridges sloping to the outer angles. The series increases in size and complexity towards the molars, in which the inner cusp tends to divide into two, converting the compressed crescent into a pair of sub-transverse crests, to which a small supplementary cusp or short crest is added at the postero-internal corner. Examination of this construction in *Uintatherium* in comparison with the molars of zalambdodonts and other Insectivora and early tritubercular mammals might suggest that the high cusp in both premolars and molars is the paracone plus metacone, united in the premolars, more or less separated in the molars, and that the protocone is not present at all. But this interpretation is not supported by the construction of the teeth in the Paleocene ancestors of the Uintatheres, in which the molars appear to be derived from a tritubercular type, although the premolars are much as in *Uintatherium*. The construction is at all events irreconcilable with near relationship to any of the known Taligrada, nor does it appear to be at all nearly related to that of *Coryphodon* in spite of a considerable resemblance in the premolars; it suggests a separate origin of the Dinocerata back in the Cretaceous. Yet the close correspondence in the foot structure is hardly to be explained away as due to mere parallelism, and a satisfactory interpretation of real relations of the taligrades, coryphodonts, and Dinocerata is still to be worked out. It can be done, for the skeletons of all three groups are quite completely known; but recent discoveries had made untenable the old view that they constituted three successive stages of specialization of a single broad group, and a revision of the whole evidence is necessary.

The Carnivora of the Eocene all belong to the primitive division Creodonta, distinguished originally by Cope by the separate scaphoid and lunar bones of the carpus, the small brain,

and other primitive features. They include half-a-dozen families, from one of which, the *Miacidæ*, are descended all the higher *Carnivora* of later Tertiary and modern time. Some authorities prefer to unite the *Miacidæ* with the modern *Carnivora* and regard the remaining *Creodonta* as a distinct order. But this makes it a very artificial assemblage, for the *Miacidæ* are much more nearly related to the *Arctocyoniidæ*, *Hyænodontidæ*, and *Oxyænidæ* than these are to the *Mesonychidæ*; and the *Oxycænidæ* are a family ancestral to all the others except the *Mesonychidæ*. Cope's arrangement on the whole appears simpler and more practical, and sets forth the real affinities of the several families more correctly.

The *Arctocyoniidæ* last through the Lower Eocene and then disappear. Gidley considers that they may be ancestral to the bears; but this appears to me quite impossible in view of the known geological record of the bears in the later Tertiary, which leads them directly back through *Tremarctotherium* and *Arctotherium* and *Hyænarctos* of the Pleistocene, *Indarctos* of the Pliocene, *Ursavus* and *Hemicyon* of the Miocene, to the *Canidæ* of the Oligocene. Nevertheless, the *Arctocyoniidæ* parallel the bears in several respects, in fact as well as teeth.

The *hyænodonts* are represented in the Eocene by a series of progressively specialized genera, beginning with *Sinopa*, then *Tritemnodon* and *Cynohyænodon*, then *Pterodon*, and last *Hyænodon*. The molar teeth in this series are progressively more sectorial, the premolars relatively more robust and massive. The molars are finally converted into double-bladed teeth increasing

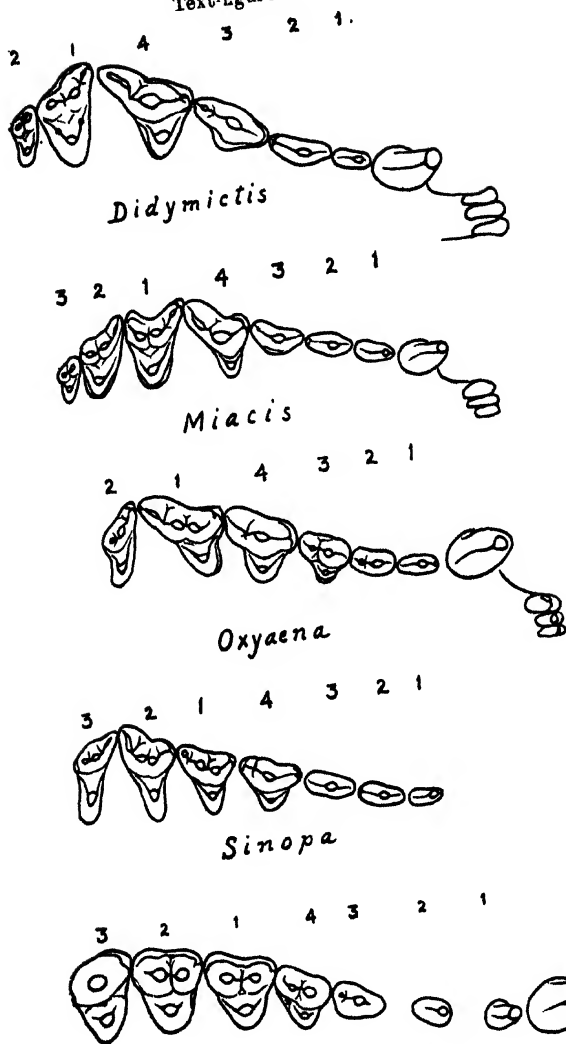
in size and shearing specialization to the carnassials $\frac{M^2}{M_3}$, while

M^3 , transverse in *Sinopa*, is reduced in *Pterodon* and absent in *Hyænodon*. These stages first appear in order of specialization, but the earlier stages survive along with their more specialized successors, and in India a genus, *Dissopsalis*, not far beyond *Sinopa* in specialization, survived into the Lower Siwalik horizon (Upper Miocene in my opinion; by Pilgrim regarded as Middle Miocene). In addition to this main line of specialization there are several side lines of less importance among the *hyænodonts* one, *Apteronodon*, with long slim skull, long jaws, and molars which have almost lost their shearing character, the cusps becoming high, round-conical, blunt-pointed, and parallel to the *Mesonychidæ* (*vide infra*).

The *Oxyænidæ*, with carnassial teeth $\frac{M^1}{M_2}$, have three distinct

phyla, evidently of diverse adaptation. *Oxyæna*, traceable through four stages in the Lower Eocene, is a powerful predaceous beast of wolverine-like proportions, and probably ancestral to the larger and more massive *Patriofelis* of the Middle Eocene, in which M^2 ,

Text-figure 12.



Pachyaena (*Mesonychidae*)

Upper teeth of Lower Eocene creodonts. Note the different positions of the carnassial notch, behind P^4 in the *Miacidae* (*Didymictis*, *Miacis*), behind M^1 in the *Oxyaenidae* (*Oxyaena*), and behind M^2 in the *Hyenodontidae* (*Sinopa*), and its absence in the *Mesonychidae*.

transverse in *Oxyaena*, has become vestigial. A smaller, more marten- or mink-like race is the Lower Eocene *Prolimnocyon* with $M \frac{3}{3}$ small, followed by the Middle Eocene *Limnocyon* with $M \frac{3}{3}$ absent, and the Upper Eocene *Oxyaenodon* with somewhat more massive teeth. This series does not change very greatly in size or in the characters of the teeth. A third phylum is the *Palaeonictis* and *Amblyctonus* of the Lower Eocene, with somewhat more specialized teeth with curiously high-pointed cusps almost insectivore-like. The adaptation of these teeth is still a puzzle; it was thought at one time that they were ancestral to the Felidæ, but this view is not now taken seriously.

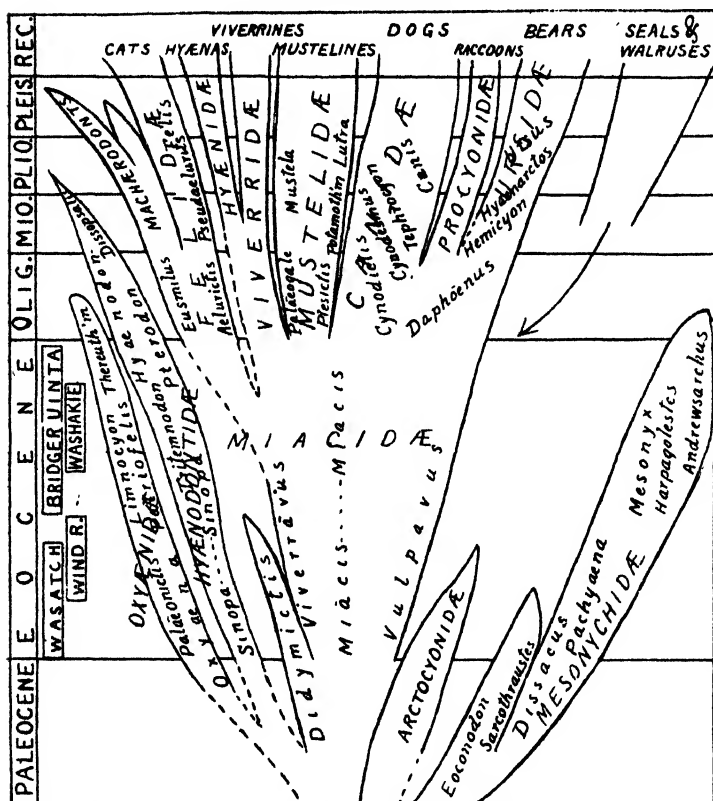
The Mesonychidæ are the most remarkable and characteristic of the creodont families. They continue through the Eocene, increasing in size to the gigantic *Harpagolestes*, as large as a Kadiak bear, and the even more gigantic *Andrewsarchus* of Mongolia, in which the skull alone was three feet long. The teeth and the proportions of the lower jaws do not change greatly; they all have high, conical cusps, generally much worn, long and rather loosely articulated jaws, and a consistently small brain-case. The head was always very large in proportion to the skeleton. The feet, in some genera at least, are proportioned much as in the modern wolves, and with small hoofs instead of claws. What the habits of this curious animal were is still a problem. It has been compared to the hyenas and called a "carrion-eater." But apart from the fact that the hyenas are not wholly or by preference carrion-eaters, but rather semi-parasitic beasts whose capacity for negotiating bones enables them to clean up profitably the remains of the kill of larger and bolder carnivora—apart from this there is really little resemblance between the Mesonychid dentition and the compact short jaw of a hyena with its powerful shearing carnassials and broad massive premolars. Whatever the food of the Mesonychidæ, it involved heavy wear of the teeth, but not great power in the jaws nor the massive premolars needed for bone-crushing, or the shearing teeth necessary to cut tendons and cut off the flesh from the bone. Turtles have been suggested as a probable prey, but this would demand shearing teeth and aquatic rather than cursorial adaptations in the feet. A diet of freshwater molluscs, *Unio*, etc., would in many respects fit the adaptation of the teeth, but a dozen other suggestions might be made, all equally plausible, all unprovable, as there is no modern analogy.

It should be remembered that in addition to the gigantic Mesonychids there were in all stages of the Eocene others of smaller sizes, down to quite small forms no bigger than a marten. Little is known about these smaller genera.

The most important group of the Creodonts is the Miacidæ, and in these we can trace a central phylum leading up rather directly into *Cynodictis* of the Upper Eocene, which is the first of the true Carnivora, and may be regarded as more or less

directly ancestral to the Canidæ, and at least approximately to the Viverridæ on one hand, the Mustelidæ on the other. From the Viverridæ in turn are derived the Hyænidæ originating in the later Tertiary, and from Middle Tertiary Canidæ the Procyonidæ and apparently the Ursidæ, although the latter may be

Text-figure 13.



Phylogenetic relations of the families of Carnivora. The Creodonts or primitive Carnivora of the Eocene included a number of extinct groups and the Miacidæ, from which the modern families of Carnivora are descended, their differentiation mostly of post-Eocene date.

traceable as a distinct phylum back to the Oligocene. The cats, while appearing to be of Viverrid affinities in the teeth, are probably a distinct group which had specialized in the Eocene from early Miacidæ and appear in the record already full-fledged at the beginning of the Oligocene. There are several side branches of Miacidæ traceable through two or three stages of specialization

in the Eocene, but the most important is *Didymictis*, paralleling the civet in its specializations; *Viverravus*, with some curiously fox-like features, although the teeth are like those of small Viverridae; *Vulpavus* and *Palaeoarctonyx*, paralleling the palm-civets in some respects. The most significant feature about nearly all the Eocene Miacidae is the relatively large brain-case as compared with other Creodonts. It was probably on account of this, rather

than any especial structural advantage in selecting $\begin{matrix} P^4 \\ M_1 \end{matrix}$ instead of

M - or M_3^2 for carnassials, that they survived and displaced the other Creodont families.

The Insectivora are rather a disappearing group during the Eocene, but are not very well known. There are a few tiny jaws that may represent the ancestors of the moles and shrews, with sharp angular cusps but still retaining the tritubercular pattern which most of the moles and all of the shrews have lost; they had not developed the specialized front teeth of the shrews; but the skull and skeleton are unknown. Apart from these there are a few small genera imperfectly known, placed among the Insectivora for convenience, but very primitive in teeth and not clearly related to any of the later Tertiary families. Zalambdodont insectivores are not known from the Eocene*, although they must have existed. The only group well understood is the Lepictidae, represented in the Lower Eocene by *Diacodon*, which seems to be directly descended from the Paleocene *Palaeolestes*, and ancestral through some imperfectly known Middle Eocene species to the Oligocene *Leptictis*, *Ictops*, and *Mesodectes*. These insectivores have tritubercular molars, a molariform P_4^1 , the front teeth somewhat on the lines of those of the hedgehog, and the skull and skeleton are quite typically insectivore and not far removed from the line of ancestry of the Erinaceidae.

The order Menotyphla, tree-shrews and their allies, is represented by a number of very tiny mammals of the *Plesiadapis* group (the "Apatemyida"), with rather specialized and reduced dentition, which can hardly be considered further here.

True Primates, lemuroids of the family Adapidae, are found in progressive development from *Pelycodus* through *Notharctus* into *Telmalestes* in America, while in Europe they progress through *Protoadapis* into *Adapis* and *Leptadapis*. Neither of these lines leads definitely into the modern lemurs, whose history is a blank from the beginning of the Oligocene to the late Pleistocene. Yet it seems probable that the ancestry of all the Malagasy lemurs must "head in" somewhere in this Eocene group, and possibly that the South American monkeys are derived from the American notharctines, although more probably they trace back to the smaller and less known tarsiid group of American Eocene Pri-

* Marsh's *Centetodon*, *Centracodon*, etc., are not zalambdodonts.

mates. This group is generally regarded as ancestral to the higher Primates, through such intermediates as the Lower Oligocene *Propliopithecus* etc. of Egypt. Whether this is entirely correct needs more and better material to prove. There are several distinct genera in the Lower, Middle, and Upper Eocene, mostly known from upper and lower jaws only, two of them, *Tetonius* of the Lower and *Necrolemur* of the Upper Eocene, from skulls. The phyletic relations are too complicated and

Text-figure 14.

*Shoshonius**Omomys**Tetonius*

Upper teeth of Lower Eocene Primates (Tarsiidae). This group of primates is regarded as most nearly ancestral to the higher anthropoids, but is as yet imperfectly known, chiefly from jaws and teeth, and appears to be nearly related to the menotyphlan insectivores of the Paleocene and Eocene (tree-shrew group).

uncertain to explain in a few words; they are fully discussed by Gregory and others*.

Rodents during the Eocene are not a very important group. They are chiefly limited to the squirrel-like *Paramys*, which runs through from Lower to Upper Eocene without much change in

* Gregory, 1920, "Structure and Relationships of *Notharctus*," Mem. Am. Mus. Nat. Hist. (n.s.) III. pp. 51-243, pls.xxiii.-xli.

teeth or skull; but to this are added in the Middle and Upper Eocene a few smaller genera, *Sciuravus*, *Mysops*, *Protoptychus*, all of doubtful affinities. The rabbits, mice, pocket-mice, beavers, etc., do not appear in the record until the Oligocene; but it is not yet clear where or when they diverged from the common ancestral stock. The rabbits and their allies must certainly have been distinct in or before the Paleocene; the simplicident rodents may all derive from the Lower Eocene *Paramys*, but the proof that they did is not yet at hand.

The edentates are represented by Lower Eocene *Palaeonodon*, which is ancestral to the Middle Eocene *Metacheiromys*, a line that may be continued through certain imperfectly known European Oligocene genera into the modern pangolins of the Oriental and Ethiopian regions. *Palaeonodon* may also be ancestral to the armadillos of the Upper Eocene and later Tertiary of South America, in which bony instead of horny armour was developed; and from the armadillos seem to have developed in turn the glyptodonts in one direction, the anteaters in another, the sloths in a third. Proof or disproof of these relations requires much more evidence, especially as to the South American armadillos, which appear first in the Upper Eocene, but are known only from a few of the armour plates until the late Miocene, at which time they are much more specialized in teeth, skull, and skeleton.

Notoungulata are represented in the Lower Eocene of North America by a single lower jaw much smaller than any of the South American notoungulates, and with a more primitive dentition than any of its allies in the Upper Eocene of Patagonia, where the group first appears in the South American succession. The North American genus *Arctostylops* is a stage further advanced than *Palaeostylops* of the Mongolian Paleocene in that the fourth premolar has become molariform. In *Palaeostylops* all the premolars are simple. In *Notostylops*, *Leontinia*, etc., three premolars are partly, two quite fully molariform. Nothing more is known of Notoungulata from the northern world, but in South America they, with the allied Litopterna, take the place of the ordinary hoofed animals and expand into numerous and varied specializations.

The tæniodonts of the Paleocene continue on through the Eocene in *Calamodon* and *Stylinodon*, paralleling the ground-sloths (whether or not they have any degree of edentate relationship) and disappear at the end of the Eocene. They are known only from North America.

Another curious extinct group, the tillodonts, is represented by *Esthonyx* in the Lower Eocene, *Anchippodus* and then *Tillotherium* in the Middle Eocene. These have a pseudo-rodent specialization in the teeth, but they are not related to rodents; whether to Insectivora or creodonts is not very clear; in any case they are best regarded for the present as a distinct order.

Tillotherium is quite a large animal, the skull and skeleton as big as that of a capybara, and the teeth are quite specialized, the incisors a single pair of perfectly-developed gnawing type, the molars low-crowned, partly bunodont, partly crested teeth, and the remaining teeth, except P_4^4 , much reduced. This is a great advance upon *Esthonyx*, in which the incisors are much more suggestive of some Insectivora in their imperfect "diprotodont" specialization. *Esthonyx* is about as large as a beaver.

Marsupials allied to the opossum existed throughout the Eocene, but call for no especial comment. They are found also in the Oligocene, both in Europe and North America—not, however, in Mongolia.

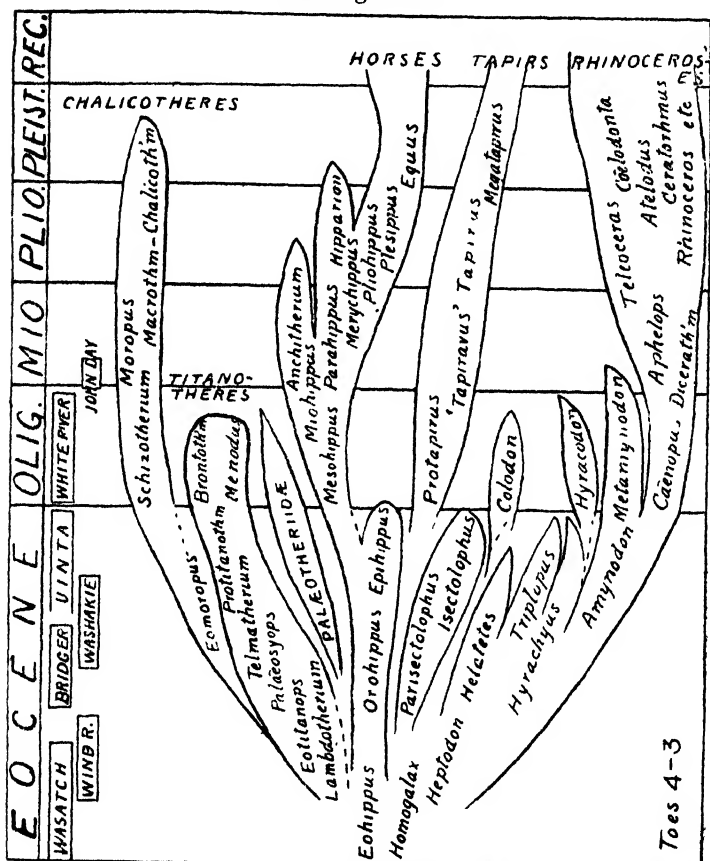
VI. The Close of the Eocene and the Oligocene Invasion.

The Oligocene opens with another great faunal invasion, bringing in many new phyla of mammals and much more progressive stages in the evolution of phyla that had already appeared in the Eocene record. A large part of the Eocene fauna disappears, becomes extinct, or is thus replaced by more advanced stages. One might suppose that this really meant a gap in the record, that a considerable lapse of unrecorded time separated the latest Eocene from the earliest Oligocene fauna. But this can hardly be so, for some of the Eocene phyla survive through into the Oligocene with very little change, and these are not all of them unprogressive or primitive types, but among them some that had been specializing rapidly through the Eocene. Another interpretation that fits better with the facts is that the later Eocene formations are found chiefly in intermontane basins, probably well forested, while the Oligocene and later Tertiary successions are recorded chiefly in plains areas which even then may have been open country. The change may be partly due to the Eocene record representing forest faunas, the Oligocene record plains faunas. But this does not wholly explain the change; and in at least one district in Wyoming where the Oligocene is directly superposed upon the Eocene, there is a change in the character of the sediment as well as in the fauna that indicates replacement of forest by open country—a change, that is, in the climate that may well have been the underlying cause of a great migration movement.

Whatever the interpretation placed upon it, the record indicates this great faunal change at the end of the Eocene, both in America and Europe, and apparently no less marked in Central Asia, as shown in the newly-discovered Mongolian fossil record. The last of the ancient groups, amblypods, condylarths, taniodonts, tillodonts, already rare and specialized types, finally become extinct. Many of the Eocene phyla of Perissodactyls and Artiodactyls disappear and are replaced by more progressive and specialized races. In the Equid lineage, the four-toed *Ephippus*

is replaced by *Meshippus* with three toes on each foot, the fifth digit of the manus, complete and still functional in *Epishippus*, reduced now to a small, short splint, quite vestigial, while the lateral digits II. and IV. in each foot have become much smaller and the central digit larger and more cylindrical. The teeth

Text-figure 15.



Phylogeny of the Perissodactyla. The differentiation of the families took place mostly during the Eocene; the surviving groups become further specialized during the later Tertiary.

also have changed considerably in pattern although still short-crowned, the change leading towards the later equid pattern. True rhinoceroses appear in Europe and America, replacing more primitive genera of less clear-cut rhinoceros affinities, and most of them aberrant or off the line of progress in one way or

another*. The Titanotheres survive into the Lower Oligocene and then become extinct; and here the change between the latest Eocene and earliest Oligocene forms is not great. The lophiodonts and other sub-tapiroid groups disappear for the most part, and true tapirs and the related colodonts, neither of them directly traceable into Eocene ancestry, take their place. On the whole, the importance of Perissodactyls in the fauna begins with a progressive decrease in the Oligocene, their place being taken by the rapidly expanding groups of ruminants.

A corresponding change is seen in the Artiodactyls at the end of the Eocene. From the confusing welter of Eocene artiodactyl races, bunodont, semi-selenodont, and primitive true selenodonts, emerge rather suddenly a number of definite, recognizable types, clearly related to the specialized groups of the later Tertiary, although some are still quite primitive. We have unmistakable pigs in the Old World, peccaries in America; camels, already quite specialized, appear suddenly at the base of the American Oligocene†, and various well-defined tragulinoids in both Europe and America, some leading up into the chevrotains, others to true deer and higher ruminants. The peculiar group of entelodonts or giant pigs appears suddenly at the base of the Oligocene, and has not been traced into the Eocene; achanodonts are probably nearly related but not direct ancestors. The oreodonts of North America, on the other hand, find fairly direct ancestors in the Upper Eocene, and the anthracothere lineages in Europe appear to be fairly direct so far as the rather fragmentary evidence shows.

The changes in the Carnivora at the end of the Eocene are equally marked. The miacid phylum carries through with but little change, but begins a rapid expansion and specialization in the Oligocene. The hyænodonts carry through, several specialized genera surviving into the Oligocene—one in India to the end of the Miocene or early Pliocene. The oxyænids and mesony-

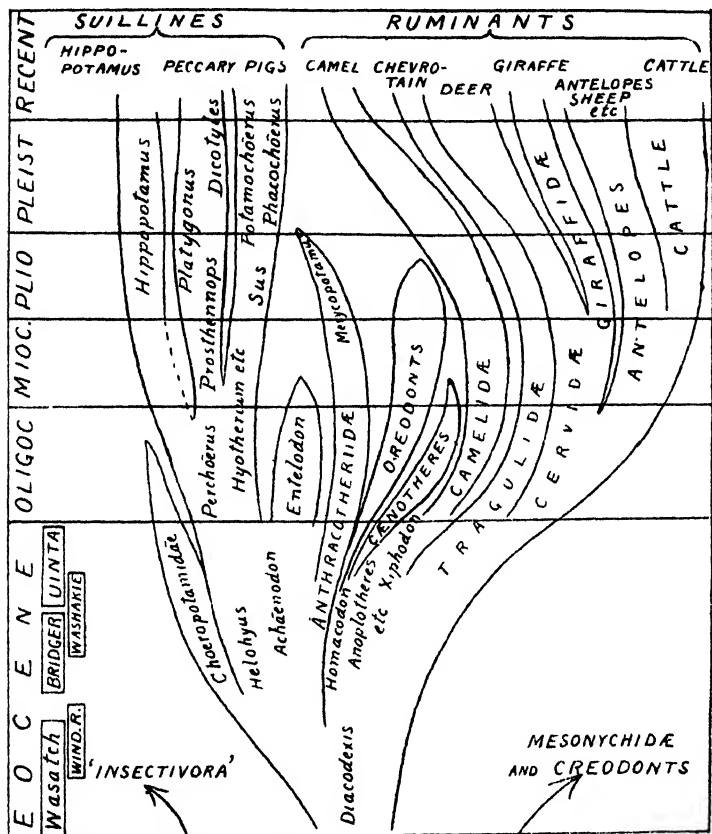
* In America the early true rhinoceroses are usually known as *Trionias* and *Cænopus*; in Europe they were formerly all referred to "*Aceratherium*," but Abel has lately provided a number of new generic names for their reception—*Prohyracodon*, *Præaceratherium*, *Prolaceratherium*, *Epiaceratherium*, *Meninatherium*. One might add also Brandt's unfortunate name of *Subhyracodon*, Cope's *Anchisodon*, and some others, all covering what are, so far as I can discover on present evidence, essentially two good genera of tridactyl rhinoceroses, one with a small complete fifth digit on the manus and more primitive premolar pattern, the other three-toed with more molariform premolars, but both distinguished by the specialized pair of caniniform incisors, lack of posterior flange on the ectoloph of M^3 , and a variety of skull characters. The Eocene rhinocerotoids have nearly all a well-developed fifth digit on the fore foot, and they have not the specialized incisors, the front teeth retaining more or less closely the primitive perissodactyl pattern of a row of small subequal incisors flanked by a pair of more or less enlarged canines.

† Current views trace the Oligocene camels *Pæbrotherium* and *Eotylopus* back into *Protylopus* of the Upper Eocene. *Protylopus*, however, when critically examined appears to be rather a primitive traguloid that might be ancestral to the higher ruminants quite as well as to the camels, but, in fact, could hardly have been a direct ancestor of the Camelidae, as it has not even the rudiments of the peculiar camelid specializations in neck and feet that are already far advanced in the *Pæbrotherium* of the Titanotherium zone. It may serve as a "structural ancestor"; a genetic ancestor it cannot well be.

chids disappear entirely; and the Felidæ first appear in Europe and America.

The insectivore record is so scanty as to be of little value, but it would appear that the principal modern group, the moles and shrews, first appears in the record at this time; the Leptictidæ

Text-figure 16.



Phylogeny of the Artiodactyla. The differentiation of the existing families is mainly of post-Eocene date.

of the Eocene carry through to the Middle Oligocene, and true hedgehogs make their first appearance.

Rodents also have a great expansion with the Oligocene. Rabbits, pocket-mice, and various other groups make their first appearance, and when the true phyletic development of rodents is more clearly understood, we shall doubtless be able to clear up the record of various other groups. At present it is clouded with too many uncertainties, improbable or untenable attempts at phyletic series, to be set forth here.

The lemuroid and tarsioid Primates that characterize the Eocene of North America and Europe are unknown from the later Tertiary of America, and disappear from the European record early in the Oligocene if not at its beginning. I do not venture to say whether they really became extinct or retreated to forested regions in more tropical latitudes where the Oligocene record is not yet discovered. From some of them, or from some allied forms which had lived in the tropical forests during the Eocene, must needs have been derived the later Tertiary Primates. But the subject is far too complex a problem to enter upon here.

In short, then, we find the Eocene epoch defined at its beginning and its close by great faunal invasions which brought about the extinction of a large part of autochthonic mammals, and replaced them by new and mostly much more progressive groups. This is the record in Europe and North America, or rather in Western Europe and the west central part of the United States, from which all records are derived. These migrations in each case bring in the same new genera to Europe and North America. They must have come from a common source, some region where these new races had been evolving and whence they spread to the regions where they appear as invading faunas. It is further evident that a marked climatic change occurred at each of these faunal changes. The most obvious and probable interpretation is that the centre or centres of evolution and dispersal of the invading races was situated somewhere in the unknown intervening region—in northern North America, central and northern Asia, and north-eastern Europe.

VII. Eocene of other Regions.

Very little is known of the Eocene Mammalia of other parts of the world. In South America a remarkable series of Tertiary faunas is known which begins with the *Notostylops* fauna, now regarded as probably of the late Eocene age, followed by a series of faunas up to the Pleistocene*. This evolution was almost wholly independent of the evolution of Tertiary mammals in the north, although derived from ancestors that must have reached South America from some northern centre about the end of the Cretaceous or beginning of the Paleocene, and supplemented probably by two or three stray invaders that would seem to have reached there at different times during the Tertiary period†.

* All these faunas were considered by Ameghino as of much greater geological age, the *Notostylops* fauna correlated with the Lower Cretaceous. Gaudry and other authorities correlated the *Notostylops* fauna with the Paleocene, on account of the relationship of a part of the fauna with the Paleocene faunas of the northern world. These elements, however, are the most primitive part of the *Notostylops* fauna, and are associated with much more advanced and progressive mammals. It appears probable, therefore, that they represent survivors little altered of Paleocene invaders from the north, and that the real age of the fauna is later, probably late Eocene. Its supposed association with dinosaurs has been discredited by later field work.

† Armadillos in the Eocene, rodents in the Oligocene, primates in the Miocene, raccoons in the Pliocene, so far as one may judge from the record.

About the end of the Tertiary, South American isolation came to an end, and a great flood of North American mammals invaded the country, resulting in the extinction of the greater part of the autochthonic mammal fauna.

The fauna lacked Perissodactyls and Artiodactyls, but developed in their place a wide variety of hoofed mammals, large and small, derived apparently from Condylarthra and Taligrada and from some of the early Insectivore groups; but the exact source needs further critical revision and surer knowledge of the exact stratigraphic succession as well as more complete specimens. At all events, the South American hoofed mammals appear to fall into at least three groups—Notoungulata, Litopterna, and Pyrotheria—all unknown to the north save for the *Palæostylops* and *Arctostylops* already discussed*.

Creodonts or any true Carnivora are wholly lacking in these South American Tertiary faunas, but their place is taken by carnivorous Marsupials, which evolved a variety of beasts of prey quite closely paralleling the northern Creodonts†.

Another group of marsupials, the cænolestids, parallel the plesiadapids in their development, and there are several other curious parallelisms to the northern faunas. But one very large group in South America was the edentates, which evolved mainly after the Eocene—at least we find no trace of them in the *Notostylops* fauna. Another important element is the hystricomorph rodents, which first appear as a single type (*Cephalomys*) in the Oligocene, and the platyrrhine monkeys, which first appear in the Miocene (*Homunculius*). These successive appearances, each apparently originating as a single type and spreading into great diversity and abundance, suggest that the isolation of South America was not so profound as has been assumed, and was perhaps largely due, as Berry has suggested, to the great tropical rain-forest and lack of environmental pressure rather than to actual oceanic barriers. The absence of creodonts, already abundant in the Lower Paleocene of North America, indicates that this isolation had begun by the beginning of the Paleocene; yet it was crossed successively by edentates, by rodents, and by primates, although not by Carnivora, Insectivora, or any of the ungulate orders until the end of the Tertiary.

As most of the known South American mammalian evolution was post-Eocene it need not be further discussed here.

* Derivation of the Pyrotheria from Paleocene Dinocerata is worth examination.

† So much so that Lydekker and other authorities insisted that they were Creodonta. Ameghino regarded them as the ancestors of the Creodonta. Their marsupial nature was proven by Sinclair in 1906. H. E. Wood has recently argued for their being specifically allied to the Australasian Thylacines; but this, in my opinion, overshoots the mark. A general relationship to the Australian polyprotodonts rather than to the Didelphyids seems to be indicated; but even this is hardly demonstrated, and the special resemblances to the Thylacines appear to be due to parallelism as I indicated in 1915. Mr. Wood brushes my argument aside with the remark that it is all within the limits of a single family—which, even if true, would not invalidate the argument. I hope later to discuss the matter more fully.

In Burma an interesting Upper Eocene fauna has recently been discovered, chiefly primitive anthracotheres, associated with titanotheres, amynodonts, and a couple of smaller Perissodactyls.

In Egypt also a few land mammals, in addition to the marine zeuglodonts and sirenians, are known from undoubted Eocene beds, but our chief light on the Eocene fauna of Egypt, and presumably of Ethiopia, comes from the remarkable group of mammals in the Lower Oligocene of the Fayûm. These include, besides anthracotheres, hyænodonts, and other Holarctic types, a variety of larger and smaller Hyracoidea, the gigantic *Arsinoitherium* and the primitive proboscideans *Mærittherium* and *Palæomastodon*, which are regarded as representing the autochthonic fauna of Ethiopia evolved and specialized during the Eocene. Probably the inference is correct enough, and will be verified by future discoveries when the African Tertiary fossil localities are adequately prospected by expert "bone-diggers." At present there is very little to add to the admirable researches of the late C. W. Andrews, but various promising localities are known and await thorough search.

The most important recent discoveries are those made in Mongolia by the American Museum Expedition in 1921-1925. As indicated in previous pages, it was expected that Mongolia would reveal the long-sought ancestors of the invading faunas that reached Europe and North America in the beginning of the Eocene and again in the Oligocene and later Tertiaries. This expectation has been only partially fulfilled. The mammal faunas found in Mongolia are correlated as Middle or Upper Cretaceous, Paleocene, Middle and Upper Eocene, Lower and Middle Oligocene, and give altogether a fair conspectus of the mammalian succession up to the Middle Tertiary.

The importance of the Cretaceous mammals has been pointed out in the early part of this memoir. The Paleocene fauna has also been discussed. The late Eocene faunas, Arshanto, Irdin Manha, and Shara Murun, have been partly described in a series of preliminary notices issued by the American Museum, but much remains to be done on them. They contain large titanotheres, amynodonts, and smaller rhinoceroses, numerous smaller Perissodactyls of lophiodont-tapiroid affinities, also a chalicotheriine, but no trace of the Equidae or Palæotheriidae. They contain tragulids that are more directly ancestral to the later higher ruminants than anything in the American or European Eocene; but there are, with the exception of a doubtful lower molar, no anthracotheres. And they include some ancestral types of Oligocene Carnivora and rodents. It is quite evident that while we may find in Mongolia the ancestry of the higher ruminants, of the rhinoceroses, perhaps of tapirs and colodonts, certainly of rabbits and pikas and probably of Dipodidae, Cricetidae, Bathyergidae, and some other rodent groups, we shall not find, as we might expect, the ancestry of other groups. These must have originated elsewhere in Holarctica, either in northern North America, northern or

southern Asia, or in eastern Europe. Perhaps their absence from Mongolia, in so far as it is not due to insufficient collections, is to be explained by the character of the fauna and of the formations in which it was found, which appear to indicate that the progressive aridity which developed during the Tertiary in all northern regions came on precociously in Central Asia, and that at the end of the Eocene the present Desert of Gobi was already an arid semi-desert country, while the Rocky Mountain region was still well watered, and western Europe mostly buried in forest. Mongolia may have been too arid for four-toed horses in the Eocene; they were perhaps evolved in the open forests of the north. It may have been equally unsuited for anthracotheres and Primates, adapted to the tropical and semi-tropical rain-forests of the Oriental region. (Egypt may then have been well watered, explaining their abundance in the Fayûm Oligocene.)

Nothing is known of the Eocene mammals of Australasia, but it is reasonably safe to infer that the deployment of the Australian marsupials had commenced as early as the Eocene. The origin of the ground-birds of New Zealand may perhaps date back to the Eocene; and it is an intriguing item of evidence that in beds supposed to be of Eocene age at Seymour Island, one of the outliers of Antarctica, remains of a group of gigantic penguins were discovered, but no mammals: suggesting that, as in New Zealand, birds developed as terrestrial vertebrates in the absence of mammals, and that the modern penguins are survivors of this old fauna of Antarctica, modified to suit the amphibious life which afforded their only chance of survival when the whole region was buried in ice.

VIII. Conclusion.

The Eocene epoch is marked by the appearance and early differentiation of the Cenozoic mammals, first adapted to forests, becoming diversified, specialized, dominant in all habitats. Evolution of the brain is a marked and important feature in the more progressive types. This becomes the most important factor of evolution. The dinosaurs of the Mesozoic had highly perfected mechanism but an inferior and unprogressive brain. This advance in brain characters means the progressive substitution of reason and conscious action for instinct and automatic action. The beginning and end of the Eocene is marked by a great change in fauna, dependent presumably upon great geographic or climatic changes, probably both associated. These are partly shown in the geologic record; but the geology of the world is not sufficiently known as yet to make these causes fully clear.

47. On some Laud Nemerteans from Upolu Island (Samoa), with Notes on the Genus *Geonemertes*. By MARY L. HETT, B.Sc., F.Z.S. (Lecturer in Zoology, Bedford College, London).

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The Nemerteans described in this paper were collected by Dr. P. A. Buxton, to whom my thanks are due for placing the material at my disposal. They were obtained from three different localities in the Island of Upolu (Samoa Islands) and at heights varying from sea-level to 2000 feet. The individuals varied in size, but on investigation they proved to be all of the same species, and must, I think, be referred to *Geonemertes palaensis* (Semper), although they differ slightly from the descriptions given by Semper (15), von Kennel (12), and Schröder (14). The last-named author has given a complete account of the species: reference will only be made here to points of special interest.

Description of Specimens.

There were in all five whole specimens and a number of pieces; in one or two instances the proboscis had become everted and broken off. The whole specimens varied in length from 15 to 40 mm., and in breadth from 0.8 to 1.8 mm. Semper (*l.c.*) gave the length of *G. palaensis* as 20 to 38 mm.; von Kennel (*l.c.*), who examined some of Semper's specimens, corrected these figures to 40–50 mm.; Isler's (11 a) specimens were 35 to 50 mm. long (though one reached 70 mm.); the single specimen examined by Schroder (*l.c.*) was 35 mm. long. Thus on the whole the specimens under consideration were smaller than the normal type. The colour (preserved specimens) was greyish on the dorsal side and pale yellow below. There was one relatively narrow dark purplish stripe in the mid-dorsal line, and in one specimen there were in addition two faintly-marked stripes, one on either side of the mid-dorsal stripe of the posterior end of the body. The rhynchostome was nearly terminal, and gave a bifid appearance to the head when the proboscis was not everted. Eyes were not visible externally, owing no doubt to loss of pigment.

INTERNAL ANATOMY.

The general features resembled those described by Schröder (*l.c.*). The following points may be noted:—

Vascular System.—The anterior termination of the dorsal vessel in a swelling below the proboscis sheath was very marked.

The lateral vessels send a branch to the dorsal vessel, and then form a commissural loop in front of the brain. There appeared to be a ventral branch on either side from this loop which extended downwards and formed a small sinus surrounding the posterior glandular portion of the cerebral organ.

Reproductive System.—All the specimens contained ovaries with ripe ova, but no testes. In two individuals sectioned, small glands were present, medial to the lateral nerves. They appeared to be gonads, but the cells were as yet undifferentiated and might have been either young ova or sperms.

Von Kennel (12) described *G. palaensis* as hermaphrodite, testes and ovaries occurring alternately and lying dorsal to the lateral nerves, with the testes ventral to the ovaries. Schröder's (14) specimens contained only ova: he therefore concluded that the species was protandrous. It is certainly an oviparous form, since in one of Dr. Buxton's specimens there is a small sac of extruded eggs attached to the proboscis.

Proboscis Nerves.—The number of proboscis nerves was 20 in two of the specimens observed and 18 in a third. The numbers given by other workers are 19 to 21.

Eyes.—In all cases there was one large pair of eyes directed forwards, but the number of smaller eyes was not constant. They were difficult to see owing to loss of pigment, but, as far as could be made out, one specimen had three pairs of subsidiary eyes, another had two pairs, while in a third only one pair could be distinguished. *G. palaensis* is generally stated to have one pair of larger eyes and two pairs of smaller ones.

With the exception of the points above mentioned, these Samoan specimens agree so closely with the descriptions given of *G. palaensis* by Semper (*l. c.*), v. Kennel (*l. c.*), and Schröder (*l. c.*) that they must be regarded as belonging to that species, but Samoa is a new habitat. Semper's original specimens came from the Palao Islands (Pelew Islands), and further specimens were found by Sarasin in Celebes and by Schröder in the Kei Islands.

It may be of interest at this point to note the close resemblance between *G. palaensis* and *G. arboricola*. The latter was described by Punnett (13) from the Seychelles in 1907, and named by him *G. arboricola* in allusion to its discovery at the base of the leaves of the screw-pine, as well as in more normal situations, such as under logs and among damp leaves. It occurred at a height of 1600 feet above sea-level. Punnett distinguished *G. arboricola* from *G. palaensis* on account of the colour-pattern and the number of eyes. In both these respects the specimens of *G. palaensis* described in the paper exhibit a type approaching that of *G. arboricola*.

(a) The coloration in both species is somewhat variable. Living specimens of *G. palaensis* are described by Semper (15) as pinkish with a dark brown dorsal stripe; the same specimens (preserved) were described by v. Kennel (12) as reddish with a blackish-brown dorsal stripe; specimens from another locality

(preserved) were described by Schröder (14) as grey-brown dorsally, lighter ventrally, with a blackish-brown dorsal stripe. *G. arboricola* was described by Punnett (13) as of a pale whitish brown with a deep purple-brown dorsal stripe and two lateral stripes at the anterior and posterior ends.

The specimens from the Island of Upolu agree on the whole with Schröder's description, but one of them has in addition a faint lateral stripe on either side of the median stripe at the posterior end, so that *G. arboricola* can scarcely be distinguished from *G. palaensis* by colour-pattern.

(b) *G. palaensis* is said to possess three pairs of eyes—one large pair directed forwards and two smaller pairs directed laterally. In *G. arboricola* all specimens have one large pair anteriorly, and in some cases a smaller pair devoid of pigment could also be distinguished, but this was not a constant feature. In the Samoan specimens of *G. palaensis* there is also some variation: as noted above, there was in each case one pair of large eyes, but the pairs of smaller eyes varied in number from one to three—so that here, too, there is no rigid distinction between the two species.

A much more important question arises in connection with the excretory system, which is said to be absent in *G. arboricola*, whereas in *G. palaensis* it is extensive. If an excretory system is really absent in the former species, this of course constitutes a very definite point of difference; but nephridia are frequently difficult to demonstrate, and it seems possible on *a priori* grounds that they may yet be discovered in the species from the Seychelles. The difference in habitat is a strong argument in favour of the two forms being distinct, but further information is desirable.

The main difficulty in identifying species of *Geonemertes* lies in the fact that some of the characters originally employed in diagnosis are now found to be of a variable nature. It therefore seemed to me useful to make a *résumé* of our present knowledge of the genus, with suggestions as to the relationships of the contained species.

Genus GEONEMERTES (Semper).

The genus *Geonemertes* was founded by Semper (15) in 1863 for the land Nemertean *G. palaensis* from the Palao (Pelew) Islands; since then a number of other land forms have been included in the genus, most of them from island habitats.

The members of this genus are relatively slender forms from 15 to 70 mm. in length (occasionally reaching 150 mm.). The coloration is variable, and in some cases there are dark longitudinal stripes. The mouth-opening is coincident with the rhynchostome. The intestinal cæcum stretches forwards nearly to the brain. The intestine is lobed. The proboscis has only one stylet sac; two to five reserve stylet sacs may be present. The number of proboscis nerves varies from 12 to 23. Nephridia are numerous and open to the exterior by many efferent pores.

The lateral nerves usually have an accessory dorsal nerve derived from the dorsal ganglion. Cerebral sense-organs are always present. Frontal organs are frequently present and well developed. One pair of larger eyes and usually one pair of smaller eyes are found, but there may be two to four pairs of smaller eyes. In a few cases the single eyes are replaced by groups of small eyes 20 to 40 in number. Reproductive organs vary in arrangement: some species are hermaphrodite and others of separate sexes.

List of Species.

G. PALAENSIS Semper, 1863 (15). Length 15 to 70 mm. (occasionally reaching a length of 160 mm.). Reddish with a single dark brown dorsal stripe. Numerous nephridia extending throughout the body, with numerous excretory pores. Hermaphrodite. 2 to 4 reserve stylet sacs. 18 to 21 proboscis nerves. One pair of large eyes and one to three pairs of smaller eyes. Habitat: Palao (Pelew) Islands, Celebes, Kei Islands, Upolu Island (Samoa Islands).

G. AGRICOLA Willemoes-Suhm, 1874 (16). Length 15 to 150 mm. Whitish or orange. Nephridia numerous, especially at the anterior end, where they are united by longitudinal canals; about 15 excretory pores on each side. Hermaphrodite and viviparous. 2 reserve stylet sacs. 13 to 15 proboscis nerves. 2 pairs of eyes. No lateral accessory nerve. Cerebral sense-organs small. Habitat: Bermudas.

G. CHALICOPHORA v. Graff, 1879 (9). Length 12 mm. White, anterior end reddish. Two longitudinal nephridial canals with numerous branches; 5 excretory pores on either side. (?) Hermaphrodite. 2 reserve stylet sacs. 12 proboscis nerves. 2 pairs of eyes. No lateral accessory nerve. Cerebral sense-organs small and lacking a glandular portion. Habitat unknown.

G. RODERICANA Gulliver, 1879 (10). Length 25 to 75 mm. Dark green dorsally with fine white lines, ventral surface white. Nephridia not yet observed. Sexes separate. 4 reserve stylet sacs. 1 to 2 pairs of eyes. 19 to 21 proboscis nerves. Habitat: Roderiguez.

G. AUSTRALIENSIS Dendy, 1889 (6, 7). Length 40 mm. Yellow or brownish, occasionally with one or more brownish dorsal stripes. Numerous nephridia extending throughout the body, opening to the exterior by numerous pores. Lateral blood-vessels connected with an anastomosing vascular network. Sexes separate. 2 to 5 stylet sacs arranged in two groups. 16 to 19 proboscis nerves. About 40 eyes in two groups. Habitat: Victoria, Australia.

G. NOVO-ZELANDIÆ Dendy, 1894 (8). Length 37 to 53 mm. Yellow with 4 broad dark bands. Nephridia not observed. Sexes separate (?). 4 reserve stylet sacs. 13 to 17 proboscis nerves. 2 pairs of eyes. Habitat: New Zealand.

G. GRAFFI Bürger, 1896 (2). Length 150 mm. Light brown with 4 dark brown stripes. Nephridia not observed. Sexes separate (?). 2 reserve stylet sacs. 23 proboscis nerves. 2 pairs of eyes. Habitat: New Guinea and Samarai Island (off New Guinea).

G. MICHOELITZI Bürger, 1896. Syn. *G. graffi* Bürger.

G. ARBORICOLA Punnett, 1907 (13). Length 15 to 25 mm. Whitish-brown with a purple-brown stripe. Nephridia absent. Hermaphrodite. 4 reserve stylet sacs. 19 proboscis nerves. 1 to 2 pairs of eyes. Habitat: Seychelles.

G. CLECA Darbishire, 1909 (5). Length 10 mm. Pale cream-colour. Nephridia not observed. Single specimen was a female. 5 reserve stylet sacs. 17 proboscis nerves. Eyes wanting. Habitat: Enderby Island (Auckland Islands).

G. SPIROSPERMIA Darbishire, 1909 (5). Length 15.5 mm. cream-coloured with dark brown stripes. Nephridia not observed. Single specimen was a male. Spermatozoa spiral. 4 reserve stylet sacs. 18 proboscis nerves. 2 pairs of eyes. Habitat: Auckland Islands.

G. DENDYI Dakin, 1915 (4). Length 15 mm. Brownish-pink, paler laterally with two chocolate-brown stripes. Nephridia not observed. Single specimen was a female. Number of proboscis nerves not stated. About 16 eyes arranged in 4 groups, 5 or 6 eyes in each anterior group, 3 in each posterior group. No well-developed cephalic gland. Habitat: W. Australia.

G. HILLI Hett, 1924 (11). Length 23 to 45 mm. Purple-brown dorsally with two bright-red lateral bands extending over the anterior two-thirds of the body; posterior end dark; ventral surface light mottled brown. Nephridia numerous and extending throughout the body, opening to the exterior by numerous pores. Lateral blood-vessels connected with an anastomosing vascular network. Sexes separate. 5 reserve stylet sacs. 18 proboscis nerves. About 80 eyes arranged in four groups, 30 eyes in each anterior group and 10 in each posterior group. Cephalic gland small or wanting. Habitat: N.S. Wales, Australia.

Examination of the species now included under the genus *Geonemertes* makes it clear that some kind of further subdivision is necessary, even if the resulting groups are not of generic value.

Such a grouping has already been suggested by Punnett (13) on the following lines :—

(1) Unstriped forms with no accessory lateral nerve, with a small number of proboscis nerves (12 to 15) and possessing an excretory system. This group would include *G. agricola* and *G. chalicophora*.

(2) Forms with dorsal stripes, with an accessory lateral nerve, and with a larger number of proboscis nerves (18 to 25); devoid of an excretory system. This group would include *G. palaensis*, *G. graffi*, *G. rodericana*, and *G. arboricola*. Not far removed from these are *G. australiensis* and (possibly) *G. novo-zelandiæ*, the former possessing an accessory lateral nerve and 18 proboscis nerves, but being also provided with an excretory system.

Since Punnett's paper, four new species have been described :—*G. dendyi* Dakin (4) and *G. hillii* (11) (both of which are closely allied to *G. australiensis* Dendy); *G. spirospemia* Darbshire (5), a striped form with 18 proboscis nerves and an accessory lateral nerve; and *G. cæca* Darbshire (5), without stripes, possessing an accessory lateral nerve and 17 proboscis nerves.

As noted above, some of the characters which were at first chosen for purposes of diagnosis are now discovered to be variable. This was pointed out by Darbshire (*l.c.*), who showed that the number of proboscis nerves and of reserve stylet sacs was not a constant one, but varied within certain limits for some, if not all, species. For example, the number of proboscis nerves originally figured for *G. australiensis* was 18, and this was used as a diagnostic character, whereas, in point of fact, further research reveals the fact that the number varies from 16 to 19.

Another source of error has been the failure in some cases to recognize the presence of an excretory system. For example, Semper (15) described *G. palaensis* as devoid of an excretory system, but the nephridia were subsequently discovered and figured by Schröder (14).

Any grouping can only be made provisionally in our present state of knowledge of the genus, but I would suggest the following arrangement :—

GROUP A.

Forms with an accessory lateral nerve and numerous nephridia opening by a large number of nephridial pores to the exterior. Blood-vessels unbranched. Two to four pairs of eyes. One or more dorsal stripes.

G. palaensis, *G. rodericana*, *G. graffi*, *G. arboricola*, (?) *G. novo-zelandiæ*, (?) *G. spirospemia*.

GROUP B.

Forms with an accessory lateral nerve and numerous nephridia with a large number of nephridial pores. Blood-vessels branched.

Numerous small eyes in two groups. Dorsal stripes inconspicuous or wanting.

G. australiensis, *G. dendyi*, *G. hillii*.

GROUP C.

Forms lacking an accessory nerve, the nephridia united by paired longitudinal canals and with a relatively small number of nephridial pores (5 to 16) on each side. Blood-vessels unbranched. Two to four pairs of eyes. Unstriped.

G. chalicophora, *G. agricola*.

Incertæ sedis.

G. caeca.

It will be seen that the presence of an excretory system (regarded by Punnett (13) as one of the distinguishing features of *G. chalicophora* and *G. agricola*) cannot be considered as diagnostic of Group C, since an excretory system is now known to occur also in *G. palaensis* and others; nevertheless, the two species mentioned above are marked off from all the rest by the arrangement of the nephridia as well as by the absence of an accessory lateral nerve.

A full account of the anatomy of *Geonemertes* has been given by several authors, notably by v. Graff (9), Coe (3), Böhning (1), and Schröder (14); hence it will only be necessary to discuss the points of special interest.

Habitat.—Reference to the list of species on pp. 190-1 will show that they are nearly all island forms, occurring in moist situations from sea-level to a height of some 2000 feet. As noted above, *G. palaensis* is the only form which has a wide distribution, the other species being described from one locality only. The species belonging to Group A are from Malaysia, N. Zealand, the Auckland Islands, Polynesia, and the Madagascar region; those of Group B from Australia; of those in Group C, one (*G. agricola*) occurs in the Bermudas, while the habitat of the other (*G. chalicophora*) is unknown. It has been suggested that *G. chalicophora* may be an Australian form because it was found in the hothouse at Stuttgart in a pot containing *Corypha australis*, which is an Australian palm; but of course there is nothing to prove that it was not introduced from elsewhere. It seems more likely that it may prove to be a New World form, seeing how closely it resembles *G. agricola* and how much it differs from the other Australian species. Coe suggests that *G. agricola* may not be indigenous to Bermuda, but introduced by plants; if this should be so, then we still need evidence as to the habitat of both these species.

The whole question of the occurrence and distribution of *Geonemertes* is thus somewhat obscure. The three undoubted Australian species constituting Group B are evidently closely

allied, and differ considerably from the rest. But the original habitats of *G. chalicophora* and *G. agricola* (Group C) are not known with certainty, while the members of Group A are scattered over a wide area stretching from the Seychelles to the Samoa Islands. The facts of distribution suggest that in some cases the species have been introduced with plants or in some similar manner, as in the case of *G. chalicophora*; but our knowledge is at present very incomplete, and further search will probably reveal the presence of *Geonemertes* in many other localities.

Size.—This is found to be variable in those species where a number of individuals have been observed, and therefore this variability probably occurs in other species as well: e. g., *G. palaensis* is stated to vary from 15 to 70 mm. in length, while *G. agricola* ranges from 15 to 150 mm. in length. In some cases this is due to sex differentiation, the males (or, in hermaphrodite forms, worms in the male condition) being smaller than the females. In *G. agricola*, which is viviparous, Coe (3) suggests that in some cases the difference was due to the fact that the worms became much reduced in size after the extrusion of embryos.

Eyes.—In most species of *Geonemertes* there is an anterior pair of larger eyes and a smaller posterior pair. The latter are sometimes difficult to recognize in preserved specimens (even in sections) owing to the fact that the pigment is removed to some extent by alcohol. Divergence from the usual condition is found in three directions:—

(a) More than one posterior pair of eyes may be present, as in *G. palaensis*, where there are stated to be three pairs in all—one large pair directed forwards and two smaller ones directed laterally. In the specimens from Upolu Island described above there was some variation; the eyes were not recognizable in the whole animal, but three specimens were sectioned—in each case there was a large pair of eyes directed forwards, but in one specimen there were three pairs of smaller eyes, in another there were two pairs, and in a third only one could be distinguished. The specimens agreed so closely in other respects that they cannot belong to other species, and one can only conclude that the number of smaller eyes is variable.

(b) Instead of two pairs of eyes there may be present two groups composed of numerous small eyes. These smaller eyes are of the same general structure as in the larger type, but relatively simpler. The groups, like the paired eyes of the species, consist of an anterior larger pair and a posterior smaller pair, the constituent eyes of each group having apparently arisen by subdivision of the original single eye. This arrangement is found in *G. australiensis*, *G. dendyi*, and *G. hillii*.

(c) Eyes may be entirely lacking, as in *G. caeca*.

Excretory System.

In seven out of the twelve species an excretory system has not so far been discovered. It is definitely stated to be absent in *G. arboricola* Punnett, while it was not observed in *G. rodericana*, *G. novo-zelandica*, *G. graffi*, *G. caeca*, *G. spirospemia*, and *G. dendyi*. An excretory system is present in *G. chalicophora*, *G. agricola*, *G. palaensis*, *G. australiensis*, and *G. hillii*. It seems probable that further investigations will reveal the presence of nephridia in most, if not all, species of *Geonemertes*. The flame-cells and ducts are sometimes difficult to identify owing to their fine structure and slight staining properties, and the ease with which they may be overlooked or misinterpreted is illustrated by the history of observations on the subject. In three species the original observers failed to find an excretory system; but it was subsequently discovered by other workers, viz. by Schröder (14) in *G. palaensis* Semper, by Coe (3) in *G. agricola* Willemoes-Suhm, by Böhmig (1) in *G. chalicophora* Graff. In *G. australiensis*, Dendy (7) recognized the presence of flame-cells, having identified one in a living condition with the cilia in action; but he could not discover their presence in his sections. I was able (11) to demonstrate the presence of an excretory system in this species, owing to the courtesy of Prof. Dendy, who supplied me with additional specimens from his collection, which I sectioned. The nephridia were very small, but they proved to be of a similar type to those which I had already discovered in *G. hillii*, and the general arrangement resembled that described by Schröder in *G. palaensis*. In the latter, however, the "flame-cells" were much longer and more easily recognizable, and they were quite obvious in most of the specimens of *G. palaensis* from Samoa. As in other Nemerteans, the terminal swellings in this species are multicellular; they were described and figured by v. Kennel in 1878, but their true nature was only demonstrated by Schröder in 1918. They are characterized by a very distinctive series of circular bands and by two conspicuous cells forming the base of the "flame." In *G. chalicophora* and *G. agricola* the nephridial tubules are united by a pair of short longitudinal canals, and there are a limited number of excretory pores opening to the exterior. But in the other cases, i. e. in *G. palaensis*, *G. australiensis*, and *G. hillii*, there appear to be no such canals present, and the nephridia, which are exceedingly numerous, open independently to the exterior.

Reproductive System.

The sexes may be united or separate, and one species (*G. agricola*) is viviparous. Observations on the actual conditions are very incomplete and confusing.

The evidence seems to be conclusive with regard to four species only:--

G. agricola, which is hermaphrodite and viviparous.

G. australiensis and *G. hillii*, which are of separate sexes and oviparous.

G. palaensis, which is hermaphrodite and oviparous.

The most complete observations so far made were carried out on *G. agricola* by Coe (3), who collected numerous specimens at different times of the year. The following conditions were found:—

1. Small specimens completely filled with ripe spermatozoa.
2. Large specimens with developing ova.
3. Very large specimens with developing embryos.
4. Large specimen with developing embryos, and, in addition, ovaries with immature ova and testes with ripe sperms.
5. Individuals with undifferentiated sexual glands which produce both ova and spermatozoa—in addition to differentiated gonads which produce ova or sperms only.

This great variety of conditions shows that it is impossible to make statements as to the arrangements of the sexual organs in any species without investigating a large number of individuals and obtaining some idea of the life-history.

In *G. australiensis* a number of specimens were obtained which were all of one sex, either male or female—the same condition was found in *G. hillii*, though in the latter case only a few individuals were found. In *G. dendyi*, which closely resembles these two species, the sexes are also said to be distinct.

In *G. palaensis*, v. Kennel (12) described and figured an hermaphrodite condition, his specimens containing well-developed ovaries and testes lying above the lateral nerve-cords. Schröder's (14) specimens contained ova only, from which he concluded that the worm is a protandric hermaphrodite. Dr. Buxton's specimens contained well-developed ovaries and also young gonads which might have been either ovaries or testes, lying both above and below the lateral nerve-cords.

Of the remaining species: (1) *G. arboricola* is said to be hermaphrodite, and a figure shows ova above and testes below the nerve-cords. (2) *G. chalicophora* was described as hermaphrodite by v. Graff (9), but Böhmig (1), who examined some of Graff's specimens, says that this was an error, and that the structures figured by v. Graff as testes were in reality young ovaries. Böhmig's own specimens contained ova only. (3) *G. rodericana* is said to be dioecious, but more information is required for confirmation. (4) *G. graffi*, *G. novo-zelandiae*, *G. cæca*, and *G. spirospemia* were described from single specimens—the first three contained ovaries only, the last contained testes only, but in the absence of further observations there is nothing to show whether these species are dioecious or hermaphrodite.

From the foregoing account it will be clear that there are still many gaps in our knowledge of the genus as a whole, and that additional information is required both as to its distribution and to important details of structure in many of the species

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48. Notes on *Hirudo medicinalis*, the Medicinal Leech, as a British Species. By W. N. BLAIR, F.Z.S.

[Received May 16, 1927: Read November 1, 1927]

Mr. W. A. Harding, in a paper entitled "A Revision of the British Leeches," published in 'Parasitology' in June 1910, states of this leech that "it is extinct in this country" and that "there is very little doubt that it no longer exists in a wild state," although it was not at all uncommon in several parts of the country about fifty years ago.

In 1909 I had been bitten by a leech which I had preserved, but not attaching any importance to my find, had not taken any trouble to record it. However, when the article was brought to my notice in November 1910, I wrote to Mr. Harding and enclosed my one example for identification. He replied that mine was a genuine *H. medicinalis*, but he was quite sure that it was an escape, or a used leech thrown away by a doctor, and that, as he stated in his recent work, it was extinct as a British species, and I should not be able to find any more. He refused to accept my offer to go with me to look for them as he was "not going to waste his time on a wild goose chase." So I went alone, and sent him about twenty of all sizes, sufficient to convince him that they bred in the locality, which is the New Forest, Hampshire, about 100 miles in area, where they are to be found in most ponds and streams.

Since 1911, therefore, I have given a considerable amount of study to their life-history, and now give some results of my research.

The leech being hermaphrodite, the act of copulation, which usually takes place about a week after a full meal, may be either single or mutual. I have had both, but have never been able to get a British and a foreign leech to copulate.

In June 1912 I isolated two which I had seen *in copula*, fed one, and she deposited a cocoon at the end of July; both were again fed late in September before hibernation, and when the first was fed in the following May, she deposited two more cocoons; they were both fed again late in the year for hibernation, and the second one, having another meal in May 1914, laid her first cocoon, *i. e.* about 23 months after the actual act of copulation. (They hibernate from about September to May.)

The cocoons are deposited by the wild leech in hollows in the moss and grass or near stones at the side of the pond or streams, and the leeches are also stated to make excavations in the clay, but I cannot confirm this.

The average size is about that of a pigeon's egg but varies with the age of the parent, as do also the number of cocoons laid and the number of eggs in each. When first deposited the cocoon is surrounded by about two cubic inches of white froth, which gradually dries up or solidifies, and turns brown, the colour of the cocoon itself.

In 1912 I cut one egg-case open as soon as laid, and found it full of a slimy liquid containing a few specks of jelly, the eggs. After a few days they had an amoeboid movement, able to move about in any direction in the liquid; in about a week their motion was planarian like, and it was three weeks before they developed the anal sucker, and the true leech form and marks became defined later. In about six weeks they were able to force their way through the cocoon and had a meal the first day. It seems remarkable that, as long as some of the liquid is left in place inside the cocoon, the development of the young leech does not seem to be retarded, notwithstanding almost daily examination, but if removed before being fully formed the embryo cannot survive, nor, apparently, if not fed within about a week of normal separate existence.

Young leeches when wild feed on frogs, tadpoles, and small fish, and it is surprising to find the number of such lying dead in the ripple marks of ponds or streams, all with the characteristic scar somewhere on them. In captivity they will feed, as soon as they emerge, on the thin skin of the human body. When adult they feed, in natural circumstances, on horses and cattle when these enter the ponds to drink; as the animals leave so the leeches drop off, some a fair distance away, which is no doubt one means of their survival. Eels and lampreys which occur in the same waters are probably enemies.

When newly hatched they require a meal about once a fortnight, until their first hibernation; in the second year about once a month; every three months in the third year, and when adult only once a year, but unless they are fed before hibernation they very often do not survive the winter. They are large enough to be used medicinally at their third year if previously well fed, but do not, I think, become sexually mature until their fourth year. They grow through life, some very large specimens I have seen being over a foot long when swimming, and I should say, about ten years old.

As to the smelling sense of leeches, from my own experience, it is the vibration of the mud in which they lie buried that rouses them and the motion of the water that attracts them, and not any sense of smell, as the water can be disturbed with a stick and no leeches will come to the surface; but on entering the water to paddle and so vibrating the earth they *may* come around by *hundreds*—some will actually leave the water as the hunter goes on dry ground. Although almost incredible, I have seen this. (I have caught 250 of a saleable

size in one hour from one pond.) Even after disturbing the mud, they can, with a stick, be made to swim away from the leech-hunter while still in the water.

The best way to catch them is by this very unscientific method, paddling and catching them by hand scissorwise in the fingers, when they immediately contract. If put at once into a damp canvas bag trailing in the water, leaving the water at intervals to transfer those caught to a tin filled with wet bogmoss, any considered too small for use can be then thrown back for next year. The very small ones are a nuisance, as they can pierce the skin well below the surface of the water, and when the mud is disturbed and the water is clouded they have a habit of getting between the toes to draw blood; the large ones, however, do not seem able to get sufficient suction until they climb to the moist skin of the leg *just above water-level*. At any rate, I have never been bitten by a mature leech while paddling, as I have been able to pick any off my legs before they reached the surface. They need about twenty seconds before they can cut through the skin.

In wet mild weather leeches frequently leave the water and travel over land from one pond to another. On one occasion, in transferring my catch from the bag to the tin, I dropped one without noticing it, and although it was a very hot day the leech made for the water; as I was enjoying a smoke I felt a prick on my leg, and saw this leech having a meal in the sun after being on dry ground for about twenty minutes and covering two yards of dry sand.

Living blood is not essential as food to this leech, as when I have had some in captivity which were too large to feed on myself I have found that they will readily pierce a length of sheep or pig intestine full of congealed blood obtained from a slaughterhouse; in fact, I have known obstinate cases to thrive if put into a vessel of bloody water for a short time once a month, which seems to prove that they can gain nourishment through their whole surface. As is the case with the mosquito, mammalian blood seems to be absolutely necessary before copulation and the deposit of a fertile cocoon.

The colour and markings of mature leeches vary very much, but all varieties may be found in the same pond. The ground-colour varies from a rich chocolate-brown to a bright green, and the typical markings, brown splashes in yellow longitudinal lines, may appear as brown spots or as a continuous brown line, or the yellow lines may be absent.

As to cannibalism, Ébrard, a French authority, has never known it, but I have had one actual instance of a leech, fullfed, being bitten by another; I do not think this is likely to happen in a wild state with plenty of open water and food. The bitten one died within two days, although I tried to heal it with newskin, perhaps *because* I did.

As regards infection conveyed by the bite, there is, I believe, one German instance of syphilis being conveyed by this means, but usually a leech after being used medicinally is thrown away or burnt, so that authentic cases are likely to be rare.

They apparently hibernate in clusters of a dozen or more, all sizes, in hoof-marks or holes under the mud, and take turns in aerating the water in mild weather.

In 1916 while in the Army I found a market for one afternoon's catch of seventy as a result of one hour's work; then I went overseas, but after demobilisation in 1919 I supplied a thousand to the trade, but was forced out of the market when the French specimens came in again in October 1919.

The British leech seems to be stronger than the continental, as I have often found that a bite is followed by rather severe inflammation which may last for four days. For instance, when bitten on the finger by a small one the whole forearm was swollen for this time, and a bite on the calf of the leg meant a swollen ankle for four days afterwards; this, however, may have been due to my attempts to cauterise with crude permanganate of potash crystals, thus retaining within the system the substance, hirudin, which is injected into the bite to prevent coagulation, although it was not the case with foreign leeches. A mature leech may remain attached for an hour, then it drops off, and if not stopped, the blood will continue to flow for about three hours before it coagulates; smaller ones take a correspondingly shorter time. In these cases I have had no bad after effects, even after eleven young at once have had a meal.

I have had no experience of native enemies, but have had an instance of some of a brood being eaten by the fish (carp) on which I attempted to feed them; but none that I have had died a natural death in my aquaria. I have, however, known them to wander about the house and shrivel up in dark corners, and they will travel long distances if the weather is damp. In 1912 I believe I presented some to the Zoological Gardens, but owing to the lack of knowledge of the keeper they were not covered over, and before they settled down all wandered away from their Aquarium and were lost down the drains.

The Natural History Museum examples are probably all (except mine) earlier than 1865, but I suspect they may still be found in various parts of the country, although I have not been able to find any records.

EXHIBITIONS AND NOTICES.

October 18th, 1927.

Major S. S. FLOWER, O.B.E., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1927 :—

JUNE.

The registered additions to the Society's Menagerie during the month of June were 733 in number. Of these 379 were acquired by presentation, 294 were purchased, 10 were deposited, 2 were received in exchange, and 48 were born in the Menagerie.

The following may be specially mentioned :—

1 White-fronted Capuchin (*Cebus apella*), 1 Brown Spider-Monkey (*Ateles hybridus*), 1 Black Troupial (*Quiscalus lugubris*), 1 Crimson-backed Tanager (*Rhamphocelus dimidiatus*), 4 Brazilian Hangnests (*Icterus jamaicai*), 6 Tovi Parrakeets (*Brotogerys jugularis*), 3 Orange-winged Parrots (*Amazona amazonica*), 6 Yellow-fronted Parrots (*Amazona ochrocephala*), from South America, presented by H.M. The King on June 13th.

An Indian Elephant (*Elephas maximus*), from India, presented by H.H. The Maharaja of Patiala, G.C.I.E., G.C.S.I., G.B.E., F.Z.S., on June 16th.

A Bennett's Wallaby (*Macropus bennetti*), from Tasmania, presented by H.R.H. The Duke of York, on June 28th.

A Collection from Portuguese East Africa, consisting of a Wart-Hog, several Antelope and other mammals, birds, and reptiles, collected by H. B. Cott, and received on June 14th.

JULY.

The registered additions to the Society's Menagerie during the month of July were 205 in number. Of these 113 were acquired by presentation, 50 were purchased, 21 were deposited, 1 was received in exchange, and 20 were born in the Menagerie.

The following may be specially mentioned :—

2 Derbyan Parrakeets (*Palaeornis derbyana*), from China, one presented by H. C. Eustace and one purchased on July 13th.

2 King Birds-of-Paradise (*Cicinnurus regius*), from New Guinea, presented by Lady Guillemard on July 15th.

1 Twelve-wired Bird-of-Paradise (*Seleucidus ignotus*), 1 Lesser Bird-of-Paradise (*Paradisea minor*), from New Guinea, and 2 Wilson's Birds-of-Paradise (*Schlegelia wilsoni*), from Waigiou, purchased on July 19th.

4 Steamer Ducks (*Tachyeres cinereus*), from the Falkland Islands, presented by Dr. Stanley Kemp, and 5 Yellow-billed Sheathbills (*Chionis alba*), from the South Shetlands, presented by A. G. Bennett, on July 29th.

1 Robber Crab (*Birgus latro*), from Christmas Island, presented by W. Goodfellow, F.Z.S.

AUGUST.

The registered additions to the Society's Menagerie during the month of August were 338 in number. Of these 87 were acquired by presentation, 203 were purchased, 7 were deposited, and 39 were born in the Menagerie.

The following may be specially mentioned :—

1 Grevy's Zebra (*Equus grevyi*), born in the Gardens on August 4th.

1 Ocelot (*Felis pardalis*), from South America, presented by Mrs. Leonard Outhwaite on August 9th.

1 Brazza's Monkey (*Cercopithecus neglectus*), from the French Congo, presented by the Hon. Mrs. Sandeman on August 25th.

1 Chimpanzee ♀ (*Anthropopithecus troglodytes*), from the Gold Coast, presented by Arthur Haserick, F.Z.S., on August 27th.

A collection of 17 Humming-Birds from Costa Rica, comprising five species, all new to the Collection, presented by J. Spedan Lewis, F.Z.S., on August 21st.

2 Fischer's Lovebird (*Agapornis fischeri*), from Victoria Nyanza, new to the Collection, presented by G. B. Chapman, F.Z.S., on August 27th.

1 Insular Lory (*Eos insularis*), from Weeda Island, presented by Alfred Ezra, O.B.E., F.Z.S., on August 31st.

2 Komodo "Dragons" (*Varanus komodensis*), from Komodo Island, Dutch East Indies, deposited by Dr. Malcolm Smith, F.Z.S., June 15th; new to the Collection.

SEPTEMBER.

The registered additions to the Society's Menagerie during the month of September were 150 in number. Of these 62 were acquired by presentation, 37 were purchased, 11 were deposited, 2 were received in exchange, and 38 were born in the Menagerie.

The following may be specially mentioned :—

A Mountain-Zebra (*Equus zebra*) ♂, purchased on September 6th; a Burmese Elephant Cow and Calf (*Elephas indicus*), presented by Alfred Ezra, O.B.E., F.Z.S., on September 24th.

2 Crimson-breasted Conures (*Pyrrhura rhodogaster*), from Central Brazil, new to the Collection, purchased on September 5th.

A Horned Screamer (*Palamedea cornuta*), from Central Brazil, purchased on September 14th.

A Twelve-wired Bird-of-Paradise (*Seleucides ignotus*), from Salawati, and two Great Black Cockatoos (*Microglossus aterrimus*), from the Aru Islands, purchased on September 22nd.

Mr. C. H. DONALD, F.Z.S., exhibited, and made remarks upon, a series of photographs of some Indian Birds of Prey.

A NEW RACE OF ARABIAN GAZELLE.

Captain J. G. DOLLMAN exhibited the mounted head of an Arabian Gazelle, and said:—"Through the kindness of H.R.H. The Duke of York I am able to exhibit the head of a Gazelle, which appears to represent a new and undescribed race of the Arabian Gazelle. I propose to name this new island race *Gazella arabica hanishi*, after the type-locality Great Hanish Island, Red Sea.

"From the typical *Gazella arabica arabica* this form differs in having a much larger and more sharply defined nasal marking, the black hairs extending nearly all along the muzzle, whereas in *arabica* this marking is more of an isolated patch. On the forehead at the base of the horns there are two black spots, which extend down the face almost as far as the dark nasal marking.

"The general colour of the upper parts is considerably less rufous than in the typical race, and the dark flank-stripe appears to be more developed. In this latter respect it approaches one of the two mainland forms, *Gazella arabica erlangeri*, from north of Aden, but is distinguished by its far less rufous colouring and larger nasal marking.

"*Gazella arabica rueppelli*, from Syria, is a much paler animal, more resembling in colour the Dorcas Gazelle. The typical race, *Gazella arabica arabica*, came from the Farsan Islands, some two hundred miles north of Great Hanish Island, the type-locality of this specimen.

"Type: adult male, mounted head in the collection of H.R.H. The Duke of York.

"Horn-dimensions of the type: length 9 inches, girth $3\frac{3}{8}$ inches, tip to tip $4\frac{1}{8}$ inches."

November 1st, 1927.

Prof. E. W. MACBRIDE, M.A., D.Sc., F.R.S., Vice-President, in the Chair.

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a series of Cinematograph Films he had taken of the Chimpanzees now in the Society's Gardens.

Mr. D. SETH-SMITH exhibited a series of photographs of a large female Chimpanzee belonging to Mr. Herbert Whitley of Primley, near Paignton, Devonshire. She had been obtained in 1922 when her weight was 12 lbs. and she was believed to be two years old. In March 1925 she grew the first of her second teeth. In January 1927 she weighed 8 stone, and in August 1927 9 stone 9 lbs.

November 15th, 1927.

Prof. E. W. MACBRIDE, M.A., D.Sc., F.R.S., Vice-President, in the Chair.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, two living Koalas (*Phascolarctus cinereus*), now in the Society's collection.

Sir ARTHUR KEITH, M.D., F.R.S., F.R.C.S., F.Z.S., and Dr. N. A. DYCE SHARP exhibited, and made remarks upon, a collection of Gorilla Skulls.

NOTES ON THE GORILLA.

By Dr. NEVILLE A. DYCE SHARP (West African Medical Service).

The 45 gorilla skulls and the 20 chimpanzee skulls exhibited this evening were all obtained in the Mamfe division of the Cameroon. Three of the former may have come from just across the Nigerian border, where I have been able to trace their haunts for a considerable distance. Chimpanzees are found in all parts of the division, while gorillas are confined to certain well-defined areas where the terrain is steep and the altitude ranges from 1200 to 5000 feet above sea-level.

The majority of the skulls were collected by myself either from the houses of the hunters who had shot them or from the back of the compound where, after finishing his meal, the hunter had thrown them months and even years before. A few came from the local "ju-ju" houses, where they had hung in the roofs for years and had become black with smoke.

During the past year I endeavoured to make a rough census of the gorilla population of my own particular parish, which I have reason to believe is circumscribed and separate from the gorilla haunts to the east. In an area approximately 60 miles long by 20 broad I estimated the actual number of adult gorillas at 180 to 230 individuals. Owing to the difficulty of enumerating the younger members of a troop these figures must be regarded as erring on the low side.

An average troop, which for feeding purposes will habitually year after year patrol the same area of 20 to 40 square miles

consists of one old adult male, possibly one immature male, and 4 to 6 females with their young. Such a troop will remain together for years—until it is broken up by raids on its female members by some young and bold male. From native accounts this fight for female followers is one of the most thrilling and often bloody events that can occur in the forest. Here, then, is a most pronounced difference between the marital affairs of the gorilla and those of the chimpanzee. For while the gorilla is fiercely polygamous the chimpanzee is usually monogamous, and only the older members of a chimpanzee party (which to my knowledge may number 40 or more) have even two female followers. A further difference is found in the Mamfe area, where chimpanzees are very timid and only dangerous when wounded, while all male gorillas attack man on sight.

One of the most remarkable of gorilla habits is their positively human love of a bed. All chimpanzees, both male and female, adult and young, sleep in trees at heights varying from 30 to 50 feet, where they make small untidy beds somewhat like a stork's nest. In the same area gorillas also make beds for themselves, but of a far more elaborate character. The big male, however, is not arboreal, and invariably makes his bed on the ground while he sends his female belongings and young offspring up trees within sight of his bed. It is said that the old man directs his wives to their respective trees. I repeatedly tried the experiment of lying where the old male had lain, and in every case I was able to see from his couch the beds of his several wives.

The male's bed may be as much as 9 ft. by 6 ft., and it is as like a spring mattress as is possible, considering that it has to be of raw forest material. To make it, he selects, clearly with some care, a suitable site where by stretching out his long arms he can encircle, bend down, and break several young saplings of two to four inches diameter. Across these he places stout branches brought from neighbouring trees, and over the whole spreads a thick layer of leaves and twigs, so as to make a couch a foot to eighteen inches deep. At the same time, he takes care to have at one side of the bed a stout tree against which he reclines in a semi recumbent position.

His wives, in appropriate trees, select suitable forks on which, by reaching out and collecting smaller branches and leaves, they make beds three to four feet in diameter. In most beds one finds leaves and branches of several varieties, but never of trees out of reach of the tree beds. This is an important observation, for at first I came to the conclusion that the material for the female beds was passed up to them from the ground, presumably by the male. My hunters so derided this idea that I examined a large number of tree beds with care and found it was always possible, given a long enough reach, which the gorilla happens to have, to stretch out and secure the varied assortment of branches and leaves which I found in each bed.

In scanty forest the bedding is correspondingly scanty. On

one occasion, just before I arrived in the village, four gorillas had slept in a plantain farm twenty yards from the chief's house. The chief it is true passed an uncomfortable night, but so did the gorillas judging by the scantiness of their beds, which were all on the ground and were made not of plantain leaves but merely of that year's weeds and undergrowth.

It was noticeable at all the beds which I examined—a number ranging between 70 and 80—that the bed itself was always kept free from droppings, although it was only to be used for one night. I estimated the weight of the droppings close under the bed of a large male at 25 to 30 lbs. It seems certain, at least in the area to which I am referring, that a new bed every night is the invariable rule. This was especially striking on the occasion when I secured the photographs which I exhibited, for a party of seven gorillas which included two young ones was confined in a small area by torrential rains which had rendered the streams on all sides impassable. Two foolish young gorillas of about 4 to 5 years of age had tried to cross and were swept away, and their broken bodies were recovered just opposite my rest-house three miles down stream. The party were therefore compelled to remain for a week in a very confined area, yet they persisted in making themselves fresh beds every night, and with care it was possible to date each bed though many were contiguous. The old male moved his bed site a few yards each night, while the females merely occupied different portions of the same trees.

It was reported that the only time a gorilla sleeps twice in the same bed is when the female has given birth to an infant and the latter is as yet too weak to hold on to the hair of her chest. The baby *gorilla* is carried on the chest, the baby *chimpanzee* rides on its mother's back. I have seen a female chimpanzee at very close quarters with two little ones running beside her and a baby on her back hanging on to her neck.

The gorilla is essentially vegetarian though he is fond of grubs and caterpillars. His main food, of which he requires a most prodigious quantity, is derived from the growing point of a species of scitamin which resembles the sugar-cane and of which he also chews the long stems. When he has a chance of a feed on a plantain farm (and I am convinced that he prefers secondary bush to virgin forest and deliberately seeks out the haunts of man to secure the aftermath of cultivation—the scitamin for instance) he neglects the fruit in favour of the stem, which he tears into ribbons in order to secure the succulent heart. My hunters assured me that the gorilla will not eat the plantain fruit, because, except when overripe, he is unable to remove the skin, which contains a white sticky latex.

I believe it an established fact that the gestation period of the gorilla is 9 months. In the Mamfe district, infant gorillas are most commonly seen at the time of the early rains, which occur about February or March. This might suggest a rutting season,

which would, however, be out of keeping with the known habits of the gorilla.

Sir Arthur Keith has referred to some of the anatomical features of the skull, but there is, I believe, a further peculiarity which I have unfortunately been unable to verify. It applies to the great male only, and is not to be found in the female. It consists in a very pronounced preponderance in the size of the right arm over the left or occasionally in the reverse condition. The native of Mamfe who is familiar with the gorilla always describes it as the great monkey with a big right arm, and, further, when the beast is being cut up and distributed to the family, the right arm takes precedence of the left and is regarded as the finest joint after the head, while the left arm is counted as quite one of the smaller joints.

I offer this report for what it is worth, well aware that such measurements as have been secured from the bony structures in the adult male do not bear this out. Yet it cannot be denied that the right and left arms are put to quite different uses when the gorilla walks in the semi-erect position.

The chimpanzee walks on the bent up knuckles, while such gorillas as I have been able to study behave as the natives had always assured me they did—that is, they rest the palms of the hands on the ground. The imprint on soft ground shows the whole surface of the palm and the four fingers only, and often merely the tips of these, while the thumb is kept flexed ready for grasping small objects such as sticks. The curiously remote position of the thumb deprives the gorilla of the powerful grasp which he would otherwise possess, and this is a point of no small importance to the hunter, who can often wriggle out of the grasp of a gorilla, but only rarely out of the grasp of a wounded chimpanzee.

Mr. HUGH CORR, F.Z.S., exhibited, and made remarks upon, a series of photographs taken during his recent visit to the Zambesi region to collect specimens for the Society.

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Rattus rattus diardi, 831.
 — — *mentawi*, subsp. n., 831.
Rattus sabanus siporanus, 827.
 — *surifer fragensis*, 829.
Rhamphocelus dimidiatus (z. s. l.), 1003.
Rhinoceros unicornis, 503.
Scalpellum distinctum, 750.
 — *molluccanum*, 747.
 — *rubrum*, 745.
 — *velutinum*, 743.
Scapteira knoxi, 935.
Sceliphron cormandelicum, 856.
Scelotes anguina, 943.
 — *arenicola*, 943.
 — *brevipes*, 943.
 — *bipes*, 934, 943.
 — *caffer*, 902.
 — *capensis*, 943.
 — *guentheri*, 943.
 — (*Herpetosaurus*) *anguina*, 902, 904.
 — *natalensis*, 943.
 — *tridactylus*, 943.
Schlegelia wilsoni (z. s. l.), 1003.
Sciurus lowii fraterculus, 824.
 — — *siberu*, subsp. n., 824.
 — *melanogaster melanogaster*, 821.
 — — *mentawi*, subsp. n., 822.
Scyphophyllidium giganteum,
 gen. n., 525.
Seleucidus ignotus (z. s. l.), 1003, 1005.
Simias concolor concolor, 813.
 — — *siberu*, subsp. n., 813.
Sinopa, 963, 973.
Sylvicapra coronata (z. s. l.), 796.
Tachyeres cinereus (z. s. l.), 1004.
Taniolabis, 949.
Telmalestes, 975.
Tetonius, 976.
Tetracelanodon, 955.
Tetraclita porosa japonica, 786.
 — — *stalactifera*, 786.
 — (*Tesseropora*) *rosea*, 786.
Tetradactylus leuicauda, 933.
 — *seps*, 933.
 — *tetradactylus*, 933.
Tyllotherium, 977.

- Trigonias*, 980.
Trilemmodon, 971.
Tropidosaura montana, 934.
Tupaia glis chrysogaster, 831.
 ——— *siberu*, subsp. n., 833.
Tylocephalum marsupium, 536.
 ——— *trygonis*, 537.
 ——— *uarnak*, 537.
Typhlops acutus, 920.
 ——— *bibronii*, 919.
 ——— *braminus*, 921.
 ——— *delalandii*, 917.
 ——— *lumbricalis*, 919.
 ——— *mossambicus*, 921.
 ——— *mucruso*, 920.
 ——— *nigroalbus*, 920.
 ——— *schlegeli*, 920.
 ——— *vermicularis*, 920.
- Unitatherium*, 970.

Varanus komodensis (L. S. L.), 1004.
Verruca calotheca flavidula, 772.
 ——— *intesta*, 774.
 ——— *navicula*, 778.
 ——— *rathbuniana*, 776.
Viverravus, 962.

Wortmania, 957.

Zanycteris, 957.
Zodarion, 849.
Zonurus caeruleo-punctatus, 932.
 ——— *cordylus*, 931.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.

May 10th, 1927.

Major S. S. FLOWER, O.B.E., Vice-President,
in the Chair.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, (1) a series of Photographs of young Chimpanzees now living in the Society's Gardens and (2) living specimens of Love-Birds now in the Society's Collection.

Mr. R. I. Pocock, F.R.S., exhibited, and made remarks upon, an unusually marked Leopard-skin from South India.

Mr. G. C. ROBSON, M.A., F.Z.S., exhibited a series of lantern-slides and specimens illustrating (a) a special type of *Hectocotylus* in the Octopoda and (b) a reconsideration of the function of the *Hectocotylus*.

Prof. D. M. S. WATSON, F.R.S., F.Z.S., gave a *résumé* of a paper by Dr. R. BROOM, F.R.S., C.M.Z.S., on "*Sphenosuchus*, and the Origin of the Crocodiles."

Dr. H. H. SCOTT, M.D., F.R.C.P. (Lond.), F.Z.S., communicated his papers on (1) "Neoplasm in an Indian Rhinoceros" and (2) "Two Cases of Peritoneal Neoplasm (Endothelioma)."

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

MR. CECIL A. HOARE, B.Sc., gave an account of "Schewiakoff's Keys for the Determination of the Holotrichous Ciliates," a translation of which from the Russian had been accepted for publication.

DR. F. P. STOWELL, B.Sc., Ph.D., A.I.C., Aquarium Research Fellow, communicated his paper on "The Resistance of certain Metals and Metallic Alloys to Corrosion and Solution by Sea-Water."

The next Meeting of the Society for Scientific Business will be held on Tuesday, May 24th, 1927, at 5.30 p.m., when the following Communications will be made:—

THE SECRETARY.

Report on the Additions to the Society's Menagerie during the month of April, 1927.

H. A. HARRIS.

The Skull Form and Dentition of the Primates.

W. N. F. WOODLAND, F.Z.S.

A Revised Classification of the Tetraphyllidean Cestoda, with Descriptions of some Phyllobothriidæ from Plymouth.

DAPHNE AUBERTIN.

On the Anatomy of the Land Snails (Helicidæ) *Cepæa hortensis* Müller and *Cepæa nemoralis* Linn.

The following Papers have been received:—

DR. C. A. NILSSON-CANTELL.

Some Barnacles in the British Museum (Natural History).

ROBERT GURNEY, M.A., F.Z.S.

Zoological Results of the Cambridge Expedition to the Suez Canal, 1924. Report on the Crustacea, Copepoda (Littoral and Semi-Parasitic).

P. ESSEN-PETERSEN.

New Species of Neuroptera Planipennia in British Collections.—IV.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
May 17th, 1927.

No. 289.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

May 24th, 1927.

Major S. S. FLOWER, O.B.E., Vice-President,
in the Chair.

THE SECRETARY read a Report on the Additions to the Society's Menagerie during the month of April, 1927.

Dr. H. A. HARRIS communicated his paper on "The Skull Form and Dentition of the Primates."

Miss DAPHNE AUBERTIN gave a *résumé* of her paper "On the Anatomy of the Land Snails (Helicidæ) *Cepæa hortensis* Müller and *Cepæa nemoralis* Linn."

In the absence of the Author, Dr. W. N. F. WOODLAND's paper on "A Revision of the Tetraphyllidean Cestoda, with Descriptions of some Phyllobothriidæ from Plymouth" was taken as read.

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. R. H. BURNE, M.A., F.R.S., F.Z.S., exhibited, and made remarks upon, injected preparations from the Angler-fish and the Cod, showing the presence and distribution of vessels of unknown function related to the lymphatic system.

The next Meeting of the Society for Scientific Business will be held on Tuesday, June 7th, 1927, at 5.30 P.M., when the following Communications will be made:—

Prof. J. P. HILL, F.R.S., F.Z.S.

Exhibition of lantern-slides of *Echidna* Embryos.

R. I. Pocock, F.R.S., F.Z.S.

The Gibbons of the Genus *Hyllobates*.

Dr. C. A. NILSSON-CANTELL.

Some Barnacles in the British Museum (Natural History).

ROBERT GURNEY, M.A., F.Z.S.

Zoological Results of the Cambridge Expedition to the Suez Canal, 1924. Report on the Crustacea, Copepoda (Littoral and Semi-Parasitic).

P. ESSEN-PETERSEN.

New Species of Neuroptera Planipennia in British Collections.—IV.

The following Paper has been received:—

W. N. BLAIR, F.Z.S.

Notes on *Hirudo medicinalis*, the Medicinal Leech, as a British Species.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
May 31st, 1927.

No. 290.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

June 7th, 1927.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

THE SECRETARY read a Report on the Additions to the Society's Menagerie during the month of May, 1927.

Prof. J. P. HILL, F.R.S., F.Z.S., exhibited, and made remarks upon, a remarkable series of photographs and drawings of *Echidna* and *Ornithorhynchus* Embryos.

Dr. H. H. SCOTT, F.Z.S., exhibited, and made remarks upon, the Crop-contents of two Ostriches.

Prof. W. ROWAN exhibited, and made remarks upon, a series of photographs bearing on the problem of Bird Migration.

Mr. D. SETH-SMITH, F.Z.S., gave an account of the Birds he had seen during visits to the Society's new Estate at Whipnade.

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Mr. R. I. Pocock, F.R.S., F.Z.S., communicated his paper on "The Gibbons of the Genus *Hyllobates*."

In the absence of the Authors the following papers were taken as read:—Dr. C. A. NILSSON-CANTELL, "Some Barnacles in the British Museum (Natural History)"; ROBERT GURNEY, M.A., F.Z.S., "Zoological Results of the Cambridge Expedition to the Suez Canal, 1924. Report on the Crustacea, Copepoda (Littoral and Semi-Parasitic)"; P. ESBEN-PETERSEN, "New Species of Neuroptera Planipennia in British Collections.—IV."

The next Meeting of the Society for Scientific Business will be held on Tuesday, October 18th, 1927, at 5.30 p.m.

A Notice stating the Agenda for the Meeting will be circulated early in October.

The following Papers have been received:—

W. N. BLAIR, F.Z.S.

Notes on *Hirudo medicinalis*, the Medicinal Leech, as a British Species.

H. HAROLD SCOTT, M.D., F.R.C.P., F.R.S.

Double Malignant Tumour of Thyroid and Parathyroid in an Otter (*Lutra lutra*).

Dr. A. SCHELLENBERG.

Bericht über die Amphipoden der Cambridge Suez Kanal Expedition, 1924.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should
be addressed to

P. CHALMERS MITCHELL,

Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

June 14th, 1927.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

October 18th, 1927.

Major S. S. FLOWER, O.B.E., Vice-President,
in the Chair.

THE SECRETARY read a Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1927.

Mr. C. H. DONALD, F.Z.S., exhibited, and made remarks upon a series of photographs of some Indian Birds of Prey.

A NEW RACE OF ARABIAN GAZELLE.

Captain J. G. DOLLMAN exhibited the mounted head of an Arabian Gazelle, and said:—"Through the kindness of H.R.H. The Duke of York I am enabled to exhibit the head of a Gazelle, which appears to represent a new and undescribed race of the Arabian Gazelle. I propose to name this new island race *Gazella arabica hanishi*, after the type-locality Great Hanish Island, Red Sea.

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"From the typical *Gazella arabica arabica* this form differs in having a much larger and more sharply defined nasal marking, the black hairs extending nearly all along the muzzle, whereas in *arabica* this marking is more of an isolated patch. On the forehead at the base of the horns there are two black spots, which extend down the face almost as far as the dark nasal marking.

"The general colour of the upper parts is considerably less rufous than in the typical race, and the dark flank-stripe appears to be more developed. In this latter respect it approaches one of the two mainland forms, *Gazella arabica erlangeri*, from north of Aden, but is distinguished by its far less rufous colouring and larger nasal marking.

"*Gazella arabica rueppelli*, from Syria, is a much paler animal, more resembling in colour the Dorcas Gazelle. The typical race, *Gazella arabica arabica*, came from the Farsan Islands, some two hundred miles north of Great Hanish Island, the type-locality of this specimen.

"Type: adult male, mounted head in the collection of H.R.H. The Duke of York.

"Horn-dimensions of the type: length 9 inches, girth $3\frac{3}{8}$ inches, tip to tip $4\frac{1}{2}$ inches."

Dr. H. H. Scott, F.R.C.P., F.Z.S., communicated his paper on "Double Malignant Tumour of Thyroid and Parathyroid in an Otter (*Lutra lutra*)."

Mr. R. Essex, B.Sc., gave a résumé of his paper on "Studies in Reptilian Degeneration."

In the absence of the Author the following Communication was taken as read:—JAMES W. Low, B.Sc., F.Z.S., "Contributions to the Development of the Pelvic Girdle. II. The Pelvic Girdle in the Batrachian *Hynobius nebulosus* s. *Ellipsoglossa nebulosa* Dum. et Bibr."

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 1st, 1927, at 5.30 P.M., when the following Communications will be made:—

F. MARTIN DUNCAN, F.Z.S.

Exhibition of Cinematograph-film of Chimpanzees now in the Society's Collection.

W. N. BLAIRE, F.Z.S.

Notes on *Hirudo medicinalis*, the Medicinal Leech, as a British Species.

Major R. W. G. HINGSTON, I.M.S., F.Z.S.

Field-observations on Spider Mimics.

Miss MARY L. HETT, B.Sc., F.Z.S.

Some Land Nemerteans from Upolu Island (Samoa), with Notes on the Genus *Geonemertes*.

The following Papers have been received:—

W. D. MATTHEW.

The Evolution of Mammals in the Eocene.

F. N. CHASEN, C.M.Z.S., and C. RODEN KLOSS, F.Z.S.

Spolia Mentawiensis — Mammals.

ARTHUR LOVERIDGE, C.M.Z.S.

(A) Notes on East African Birds (chiefly Nesting-habits and Stomach-contents) collected 1926.

(B) Notes on some East African Invertebrates collected 1927.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.

October 25th, 1927.

No. 292.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

November 1st, 1927.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, a series of Cinematograph films he had taken of the Chimpanzees now in the Society's collection.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a series of photographs of a large female Chimpanzee belonging to Mr. Herbert Whitley.

Mr. W. N. BLAIR, F.Z.S., communicated his paper "Notes on *Hirudo medicinalis*, the Medicinal Leech, as a British Species."

Major R. W. G. HINGSTON, I.M.S., F.Z.S., gave a *résumé* of his paper on "Field-observations on Spider Mimics."

Miss MARY L. HETT, B.Sc., F.Z.S., gave a *résumé* of her paper on "Some Land Nemertean from Upolu Island (Samoa) with Notes on the Genus *Geonemertes*."

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The next Meeting of the Society for Scientific Business will be held on Tuesday, November 15th, 1927, at 5.30 P.M., when the following Communications will be made:—

Sir ARTHUR KEITH, M.D., F.R.S., and Dr. N. A. DYCE SHARP.

Exhibition of Gorilla Skulls.

HUGH COTT, F.Z.S.

Exhibition of Photographs taken on the Zambesi.

W. D. MATTHEW, F.R.S.

The Evolution of Mammals in the Eocene.

F. N. CHASEN, C.M.Z.S., and C. BODEN KLOSS, F.Z.S.

Spolia Mentawiensis.—Mammals.

ARTHUR LOVERIDGE, C.M.Z.S.

(A) Notes on East African Birds (chiefly Nesting-habits and Stomach-contents) collected 1926.

(B) Notes on some East African Invertebrates collected 1927.

The following Papers have been received:—

PERCY ROYCROFT LOWE, M.B., F.Z.S.

Studies and Observations bearing on the Phylogeny of the Ostrich and its Allies.

B. R. SESHACHAR, B.Sc.

The Structure of the Skin in some Genera of the Engystomatid Family (Anura).

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
November 8th, 1927.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

November 15th, 1927.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, two living Koalas (*Phascolarctus cinereus*) now in the Society's collection.

Sir ARTHUR KEITH, M.D., F.R.S., F.R.C.S., F.Z.S., and Dr. N. A. DYCE SHARPE exhibited, and made remarks upon, a collection of Gorilla Skulls.

Mr. HUGH COTT, F.Z.S., exhibited, and made remarks upon, a series of photographs taken during his recent visit to the Zambesi region to collect specimens for the Society.

Prof. E. S. GOODRICH, M.A., F.R.S., F.Z.S., gave a résumé of a paper by Prof. W. D. MATTHEW, F.R.S., on "The Evolution of Mammals in the Eocene."

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In the absence of the Authors, the following papers were taken as read :—F. N. CHASEN, C.M.Z.S., and C. BODEN KLOSS, F.Z.S., "Spolia Mentawiensis.—Mammals"; ARTHUR LOVERIDGE, C.M.Z.S., "(A) Notes on East African Birds (chiefly Nesting-habits and Stomach-contents) collected 1926," and "(B) Notes on some East African Invertebrates collected 1926."

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 7th, 1928, at 5.30 P.M.

A Notice stating the Agenda for the Meeting will be circulated in January.

The following Papers have been received :—

PERCY ROYCROFT LOWE, M.B., F.Z.S.

Studies and Observations bearing on the Phylogeny of the Ostrich and its Allies.

S. ZUCKERMAN, M.A.

The Age-changes in the Chimpanzee, with special reference to Growth of Brain, Eruption of Teeth, and Estimate of Age, with a Note on the Taungs Ape.

F. F. LAIDLAW, M.A., F.Z.S., and the late H. CAMPION.

Notes on Oriental Dragonflies (Odonata) with Descriptions of New Species.

Prof. D. M. S. WATSON, F.R.S., F.Z.S.

On some Points in the Structure of Palæoniscid and allied Fish.

ENID K. SIKES, B.Sc.

The External Morphology and Life-history of the Coccid Bug *Orthezia urticae* Linn.

H. C. JAMES, B.Sc., Ph.D., N.D.A., N.D.D.

On the Post-Embryonic Development of the Female Genitalia and of other Structures in the Chalcidoid Insect *Harmolita graminicola* Gir.

H. HAROLD SCOTT, M.D., F.R.C.P., F.Z.S.

Carcinoma of the Tonsil in a Common Wolf (*Canis lupus*).

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

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P. CHALMERS MITCHELL,

Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,

REGENT'S PARK, LONDON, N.W. 8.

November 22nd, 1927.

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